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GREENHOUSE GAS FLUX SOURCES IN A YOUNG BOREAL RESERVOIR

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Avant-Propos

The present thesis contains two general abstracts, one in French and one in English, followed by a general introduction in English which presents a thorough review of the scientific literature pertaining to the subject of this thesis. The introduction is followed by two studies which present data collected in the Eastmain-1 Reservoir and regional lakes, near James Bay, Québec, in the summer of 2008. Sampling was carried out predominantly by Annick St. Pierre, Simon Barrette, Delphine Marchand, and me. The final section of this thesis is a general conclusion of our findings. The analysis and interpretation of all findings were carried out predominantly by me, my supervisor Yves Prairie, and my co-supervisor Paul del Giorgio. The first article is to be submitted to *Biogeochemical Cycles*, and the second article is to be submitted to the *Canadian Journal of Fisheries and Aquatic Sciences*.

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Abstract

Although artificial reservoirs are estimated to represent nearly 10% of all continental freshwaters, there is relatively little literature regarding the role which they play in relation to the natural carbon cycle. It is possible that this lack of research stems partly from their amorphous, unclassifiable nature; they often seem to be as temporary as they are permanent and as natural as they are artificial, sharing the physical traits of both lakes and rivers. In light of current trends in climate change, reservoirs have become increasingly studied by the scientific community in an attempt to understand and quantify the important role they play in the transport and exchange of carbon between terrestrial environments and the atmosphere. This study focuses on a young boreal reservoir (Eastmain-1) which is located in Quebec, Canada, and examines two fundamental aspects of its biogeochemical processes.

The first unit of this study compares the significance of the water column and benthic environments as sources of carbon dioxide (CO_2) in Eastmain-1 with 13 regional natural lakes. This unit concludes that the water column tends to be the primary source of CO_2 in Eastmain-1 as well as natural lakes. Furthermore, the mean relative contribution of benthic respiration towards total net CO_2 production during stratified periods was similar in both aquatic systems (23% in lakes, 26% in Eastmain-1). The second unit of this study examines the relationship between landscape heterogeneity in the boreal zone and the spatial patterning of CO_2 production and surface emissions in Eastmain-1. A significant relationship is found to exist between the pre-inundation carbon stock of a landscape and local measured post-inundation benthic respiration rates, water column respiration rates, and surface CO_2 emissions. Pre-inundation sediment and soil respiration rates of flooded ecosystems are generally found to be similar to our estimates of benthic respiration rates at associated sites within the flooded reservoir.

These findings represent a significant advancement in our fundamental understanding of carbon cycling in reservoirs, and may lead to more accurate methods by which CO_2 emissions can be estimated for a given reservoir prior to inundation.

Key words: carbon cycling, climate change, hydroelectric reservoirs, boreal, CO_2 fluxes, lake metabolism

Résumé

Les réservoirs artificiels représentent environ 10% (en surface) de toutes les eaux continentales, cependant leur rôle dans les systèmes naturels demeure largement méconnu. Ceci est en partie dû au fait que ces systèmes sont difficilement classifiables; qu'ils soient temporaires ou permanents, naturels ou artificiels, ils peuvent ressembler aussi bien à des rivières qu'à des lacs et possèdent des gradients biophysicochimiques variés. Néanmoins, dans le contexte des changements climatiques, les études se multiplient afin d'élucider leur rôle possiblement important dans le transport et la transformation du carbone ainsi que dans les échanges avec le milieu terrestre et l'atmosphère. Ici nous présentons l'étude d'un jeune réservoir boréal au nord du Québec (Eastmain-1), en examinant deux aspects importants de ces processus biogéochimiques.

La première unité est une évaluation des contributions relatives du benthos et de la colonne d'eau comme sources de dioxide de carbone (CO_2) dans le réservoir comparées à celles de 13 lacs boréaux naturels. Cette partie de l'étude conclue que la contribution du benthos est relativement constante entre les deux types de systèmes (23% dans les lacs, 26% dans le réservoir Eastmain-1) et que c'est la colonne d'eau qui est la source majeure de production de CO_2 dans le réservoir Eastmain-1 ainsi que dans lacs naturels. La deuxième partie de cette étude examine l'hétérogénéité du paysage inondé par Eastmain-1, et montre un lien direct entre le stockage de carbone d'un paysage avant inondation et la production de CO_2 observés dans la colonne d'eau et provenant du benthos, ainsi que les flux de CO_2 vers l'atmosphère.

Nous espérons que ces données pourront être utilisées pour mieux prédire les émissions de CO_2 vers l'atmosphère suivant l'inondation d'un réservoir.

Mots clefs: Cyclage du carbone, changements climatiques, reservoirs hydroéléctriques, boréale, flux de CO_2, métabolisme des lacs

Introduction

As the second largest consumer of hydroelectricity in the world (BP, 2009), it may not be surprising that Canada has played a major role in a recent global surge of interest in the ecological characteristics of artificial reservoirs. Originally, much of the research concerning reservoirs focused on their associated environmental and social impacts (Rosenberg et al., 1995; Tremblay et al., 1998). In recent years, however, the threat of global climate change linked to anthropogenic activities has spurred efforts to better understand the role played by reservoirs in transporting terrestrial carbon to the atmosphere in the form of greenhouse gases (GHGs) such as carbon dioxide (CO_2) and methane (CH_4). CO_2 is often considered of particular significance to reservoir surface emissions, as most CH_4 is frequently oxidized near the sediments (Duchemin et al., 1995). This thesis addresses the issue of reservoir CO_2 emissions in two stages. To begin, it compares the relative contribution of the benthic environment towards surface CO_2 emissions in an average-sized (600 km^2) young hydroelectric reservoir (Eastmain-1) and a regional cross-section of natural lakes. Next, this study investigates the relationship between the pre-inundation carbon stock of a landscape with CO_2 production in the flooded benthic environment and overlying water column of the same young reservoir. Each of these stages represents a chapter of this thesis.

Freshwater environments in the context of natural carbon cycles

Freshwater is estimated to make up less than 5% of the global water supply stored at any given time, and the majority of this is frozen in polar regions (Korzoun and Sokolov, 1978). It is therefore understandable that the traditional view of global carbon dynamics does not place a strong emphasis on freshwater aquatic systems such as lakes and rivers, often considering them as a purely mechanical transport pathway for terrestrial carbon towards oceans (Cole et al., 2007). It is only in the past decade that these environments have been recognized as playing a significant role in

global carbon dynamics. In fact, it is now estimated that more than half of all carbon entering aquatic systems from the terrestrial environment is deposited as sediments or released to the atmosphere as GHGs before reaching an ocean (Cole et al., 2007). As a result, the vast majority of global lakes (estimated as 87%) act as net contributors of CO_2 to the atmosphere (den Heyer and Kalff, 1998; Algesten et al., 2003). Alternately, terrestrial ecosystems such as forests and peat bogs are frequently carbon neutral or carbon sinks with respect to the atmosphere (St. Louis et al., 2000; Algesten et al., 2003). The significant role that lakes play in the carbon cycle appears to be especially pronounced in the boreal region, which is one of the largest biomes on earth (Venkiteswaran, 2002). It is estimated that boreal lakes, which constitute roughly 20% of the world's lake surface area, emit as much as 40% of the total annual CO_2 emissions of all natural lakes (Kortelainen et al., 2006).

Although freshwater lakes and rivers generally transport terrestrial carbon to the atmosphere, specific carbon emissions vary significantly, and rely upon factors such as morphometry and climate, as well as the availability of carbon and nutrients (Riera et al., 1999; Flanagan et al., 2006). Specific landscapes can differ significantly in the quantity of stored carbon as well as the primary location of such storage. For instance, the majority of carbon in tropical forests is generally stored as vegetation, while the majority in the boreal zone is stored in the soils (Malhi et al., 1999). The boreal biome is clearly an important region for any study which aims at identifying and understanding the pathways by which terrestrial carbon is stored or transported to the atmosphere by freshwater aquatic environments. Its inherent ecological heterogeneity (shaped by regular forest fires, aquatic ecosystems, and peatlands) necessitates, however, that such a study takes into account the specific characteristics of the various landscapes that a boreal reservoir inundates.

Artificial reservoirs in the context of natural lakes

As the important role of natural aquatic environments in carbon cycling has become better understood, many researchers have begun to question how artificial

reservoirs might influence regional and global carbon cycles. Impoundments and reservoirs serve a variety of purposes, ranging from irrigation to the provision of electrical energy (Venkiteswaran, 2002). The reliance of societies upon the services provided by reservoirs has grown to the point that reservoirs today hold from 10-20% of the global mean river runoff at any given time, yet their functionality as ecological systems remains largely unknown (Houel et al., 2006; Cole et al., 2007).

Beyond transforming a riverine environment to a more lacustrine one, the construction of a reservoir may alter the natural transport of carbon between the aquatic, terrestrial, and atmosphere environments in complex ways. The flooding of terrestrial environments leads rapidly to elevated GHG emissions as large stores of flooded carbon decompose, resulting in rates of carbon transport to the atmosphere which may be more than double those of natural lakes (St. Louis et al., 2000; Cole et al., 2007). The intensity and duration of CO_2 emissions, and therefore the impact that a reservoir could have on atmospheric concentrations of GHGs, appears to vary considerably depending on the location of the reservoir and the type of landscape which has been flooded (Tremblay, 2004; Bodaly et al., 2004). CO_2 emissions from reservoirs located in carbon-rich environments such as tropical and boreal regions appear be particularly elevated (Tremblay, 2004; Soumis et al., 2004), though research has suggested that carbon lability can play as important a role as carbon richness in determining surface CO_2 emissions in the first years after a reservoir's inundation (Matthews et al., 2005).

When attempting to understand the role of a flooded landscape with respect to surface CO_2 emissions, many studies treat the water column as a conduit of benthic-derived CO_2 to the atmosphere, failing to account for respiration occurring within the water column itself (Duchemin et al., 1995; Kelly et al., 1997; Matthew et al., 2005). However, various studies have reported that the water column plays a major role in reservoirs, representing from 20% to as much as 80% of surface CO_2 emissions (Aberg et al., 2004; Abe et al., 2005, Lalonde, 2009). By presenting the metabolism of a young boreal reservoir in the context of regional natural lakes, which can also

range significantly in the proportional contribution of the water column to surface CO_2 emissions (Jonsson et al., 2001; Aberg et al., 2007), it becomes possible to better distinguish the extent to which an artificial reservoir is shaped by the natural environment in which it exists.

Hydroelectricity and the boreal zone

Canada's largest hydroelectric reservoirs are located in the boreal regions of Manitoba and Quebec. The boreal belt, with the temperate zone to the south and the arctic tundra to the north, is characterized by extensive carbon-rich peatlands, lakes (comprising roughly 7% of the total surface area), and mixed coniferous and deciduous forests (Venkiteswaran, 2002; Kortelainen et al., 2006). It is estimated that, on average, the soils of the boreal region store 343 T/ha of carbon, a quantity which is roughly 2.8 and 3.6 times the levels in tropical and temperate soils, respectively (Malhi et al., 1999). The significant accumulation of carbon in boreal forests is due both to the cold climate as well as the water-logged nature of the soils, which together lead to relatively low rates of decomposition (Malhi et al., 1999). In the context of reservoir construction, these carbon-rich soils provide the potential for long-term elevated GHG emissions when flooded (St. Louis et al., 2000; Venkiteswaran, 2002). The lakes and streams located in Quebec's boreal region near James Bay are typical of those in other boreal regions in that they are consistently supersaturated in CO_2 (Roehm et al., 2009, Teodoru et al., 2009).

In order to better understand the processes which occur after a reservoir is constructed in Canada's boreal zone, a range of studies have been carried out to examine boreal reservoirs of varying ages, as well as creating experimental reservoirs which flood only specific landscapes within the region (such as a forest or peatland) (Duchemin et al., 1995; Bodaly et al., 2004; Kelly et al., 1997). One of the most significant and ambitious projects, however, has been the study of the Eastmain-1 Reservoir, which was impounded in 2005 as part of Hydro-Quebec's James Bay Project. The Eastmain-1 Project is the first study to examine natural terrestrial and

aquatic landscapes prior to the flooding of a hydroelectric reservoir, and to follow the effects of flooding on the atmosphere and inundated landscapes in the first years after impoundment. As a result, this study has provided researchers with a valuable opportunity to understand and quantify the respective roles of the benthic and water column environments in the production of CO_2, as well as examine the spatial heterogeneity of CO_2 production within the reservoir in relation to the terrestrial landscape flooded. A solid understanding of both of these aspects of hydroelectric reservoirs is important as it will facilitate increasingly accurate estimates of annual GHG emissions from Canadian reservoirs, as well as provide better tools for planning more efficient and environmentally clean energy production on a local and international scope.

Metabolic balance of a reservoir

CO_2 production in aquatic systems occurs primarily in the benthic environment (including sediments as well as decomposing terrestrial organic carbon in the case of reservoirs) and the water column. For shallow and oligotrophic lakes, the sediments may be considered an especially significant site for organic matter mineralization (den Heyer and Kalff, 1998). This is largely due to the fact that surface sediments are generally home to a lake's highest respiration rates, bacterial biomass, and concentrations of organic material (Aberg et al., 2007). In total, as much as 85% of oxygen consumption within a lake's hypolimnion occurs in its sediments, which can result in sediments being the source of as much as 50 to 80% of the total GHG emissions in a natural lake (den Heyer and Kalff, 1998; Aberg et al., 2007). As the proportional sediment area decreases with respect to the water column, however, their contribution to overall respiration rates weakens (Aberg et al., 2007).

For hydroelectric reservoirs, the influence of decomposing terrestrial organic carbon has often been the primary consideration for research into the quantity of CO_2 produced or released to the atmosphere (Kelly et al., 1997; St. Louis et al., 2000; Bodaly et al., 2004). Net GHG emissions are, however, frequently greater than long-

term carbon stock degradation would be predicted to support, suggesting that respiration within the water column could play an influential role as well (Houel et al., 2006). Estimates of annual CO_2 emissions from reservoirs are rarely made from measured CO_2 production rates within the water column or flooded soils and sediments. Instead, estimates tend to rely upon direct measurements made with floating chambers which record the accumulation of GHGs over a fixed period of time, or by estimates involving the concentration of a GHG such as CO_2 in surface waters and the atmosphere, and adjusting the diffusion rate between the two by the measured wind speed (e.g. Wanninkhof, 1992; Tremblay et al., 2004). While other methods of estimating GHG emissions from reservoirs have been utilised, including the use of eddy covariance towers (Strachan et al., 2009) and stable isotopes modelling (Hélie and Hillaire-Marcel, 2005), the use of floating chambers has been adopted as the standard and preferred method for reservoirs in Quebec (Lambert and Fréchette, 2006). The use of floating chambers in estimating surface GHG emissions has been criticized, however, for providing consistent overestimations due to the turbulence created by the device (Vachon et al., submitted). While floating chambers may overestimate surface fluxes of GHGs, any measurements of surface fluxes might theoretically underestimate the total CO_2 produced in reservoirs, as several studies have suggested that significant quantities of GHGs produced within the reservoir may escape from sources other than the water-air interface of the reservoir, such as the reservoir outflow or the river downstream (Abril et al., 2005). Furthermore, aquatic systems which are deep enough to stratify seasonally typically accumulate a store of CO_2 in the hypolimnion which is only largely emitted to the atmosphere when the water column is mixed (Duchemin et al., 1995). Direct measurements of surface CO_2 emissions taken over a short time period therefore run the risk of significantly over or underestimating total annual CO_2 emissions, depending upon the thermal stability of the water column. A full understanding of each component of GHG production within a reservoir is therefore ideal in order to gain a full understanding of the system.

Analytical methods

The first goal of this study is to quantify the contribution of respiration in the water column and benthic environment of a moderately sized boreal reservoir, and to compare the metabolism of the reservoir with the natural variability measured in regional lakes. To complete this task, data were collected in Eastmain-1 and 13 regional lakes over a four month period of 2008 which represented the majority of the region's ice-free period (ranging from June to September). Surface-water and profundal water column CO_2 production rates were estimated in all lakes and across 11 reservoir sites (each consisting of two replicate stations) by measuring the consumption of oxygen over a period of 60 hours in darkened and temperature-controlled conditions. A non-intrusive method of measuring oxygen levels using a fiber optics oxygen sensor was chosen so as to minimize the exposure of samples to atmospheric oxygen (methods further detailed in Marchand et al., 2009). The rate at which CO_2 accumulated in the hypolimnion during periods of thermal stratification was estimated in lakes and Eastmain-1 from repeated vertical profiles recording pCO_2 and temperature at intervals of 0.5 to 2m from the surface to the sediments (or 28m, the limit of the sampling equipment). In natural lakes, these profiles were taken from helicopters or hydroplanes at the center of lakes, three times over the four-month period. In Eastmain-1, simple stations involving three anchors laid over a large area (so as to minimize vertical disturbance as well as horizontal drag) were installed, and were sampled by boat from four to six times over the four month period. This sampling was organized so as to record the changes in the water column over long time periods (on a scale of roughly one month) as well as over short ones (with samplings separated by one to two days, carried out over a period of a week).

Benthic respiration was estimated in reservoirs and lakes as the difference between the rate of CO_2 accumulation in the hypolimnion and the water column respiration rate in the hypolimnion (as estimated by O_2 depletion, described above). By summing these estimates of benthic respiration with our measurements of water column respiration, and subtracting estimates of primary production derived from

chlorophyll *a* levels within the photic zone (measured spectrophotometrically in ethanol extracts, as per previous studies, e.g. Marchand et al., 2009), estimates could be made of the total net CO_2 production for natural and aquatic systems. These values could, in turn, be compared to surface flux estimates taken by floating chambers and surface pCO_2 levels in order to test the agreement between methods.

The second stated goal of this research is to align pre-inundation landscape characteristics (specifically carbon stock and soil respiration rates) with post-inundation landscape-oriented heterogeneity within the Eastmain-1 reservoir. Sampling stations installed over the 2008 ice-free period were positioned over a range of landscape types so that differences in surface fluxes, nutrient levels, and rates of CO_2 production in the water column and sediments could be quantified.

Heterogeneity of terrestrial environments

In order to compare a boreal reservoir with the landscape it has replaced, it is first necessary to account for the distinguishing features of the natural terrestrial and aquatic landscapes. The majority of the area flooded by the Eastmain-1 Reservoir (65%) was classified as boreal forest ecosystems (Teodoru et al., submitted), which is a mixed deciduous – coniferous forest located between temperate forests and the tundra (Venkiteswaran, 2002). Regular forest fires burn roughly 1% of North America's boreal forests annually, creating distinct upland landscapes with notably different areal carbon stocks (Marchand et al., 2009). The primary forest types examined in this study were two year old burned forests (occupying approximately 1% of the flooded area), 17 year old burned forests (occupying approximately 18% of the flooded area), and mature forests (occupying roughly 27% of the flooded area) (Teodoru et al., submitted). The carbon stock of the forests flooded by Eastmain-1 was estimated from measurements to be roughly 7.6 kg C m^{-2} in mature forests, 6.1 kg C m^{-2} in 17 year old burned forests, and 5.8 kg C m^{-2} in two year old burned forests (Banville et al., submitted). It is estimated that the majority of the boreal forest's most labile carbon, foliage, will have decayed after three years of inundation

(the age of the present study), though less-labile vegetation such as wood and shrubs may continue decaying for a longer period of time (Matthews et al., 2005). In the boreal zone, forests may be generally considered an upland ecosystem type, occupying higher elevations. In the context of a reservoir, forests therefore tend to occupy shallow flooded areas, and are subject to more frequent dry periods with changing water levels in the reservoir.

Roughly 21% of the area flooded by the Eastmain-1 Reservoir had been previously occupied by natural freshwater systems, including natural lakes as well as the original riverbed of the Eastmain River (Teodoru et al., submitted). Boreal lakes can range significantly in depth, surface area, and water chemistry, though lakes sampled in the immediate region of the Eastmain-1 Reservoir had surface areas ranging from 0.04 to 3.84 km^2, mean depths from 1.5 to 5.7m, and were generally humic. Regional lake sediments contain an estimated 15.2 kg C m^{-2} (Teodoru et al., submitted), which is significantly higher than river sediments, which are estimated to contain roughly 0.1 kg C m^{-2} (Jonsson et al., 2007). In the context of a reservoir, lake and river beds can generally be expected to occur at the greatest depths, and therefore sediments in these areas are likely to be in contact with cold hypolimnetic waters through most, or all of the year.

Peatlands make up the smallest spatial component of the major ecosystem types flooded by Eastmain-1 (18%, Teodoru et al., submitted), though store more carbon than any other ecosystem (roughly 112.8 kg m^{-2}, Roulet 2000; Horwath, 2008). Peatlands, which we here consider as all wetland ecosystems ranging from fens and bogs to swamps, are lowland ecosystems typically located at intermediate elevations between lakes and forests. Unlike boreal forests, which are generally considered to be carbon sinks with respect to the atmosphere, peatlands are thought to be carbon-neutral due to slight emissions of methane, a GHG over 20 times more powerful than carbon dioxide (Roulet, 2000, St. Louis et al., 2000). Being generally lowland ecosystems, in the context of a reservoir, flooded peatlands are often located at intermediate depths between flooded forests and flooded aquatic ecosystems.

Heterogeneity between different hydrodynamic regions of Eastmain-1

Upon the construction of a reservoir, nutrients and dissolved organic carbon (DOC) are released from flooded terrestrial environments into the overlying water column (Paterson et al., 1997). Furthermore, inundated vegetation is consumed by bacteria, rapidly producing large quantities of CO_2 (Matthews et al., 2005). This initial period of high productivity in a new reservoir is termed the trophic upsurge, and generally lasts for several years before being followed by the trophic decline, a period during which the reservoir is expected to produce GHGs at rates more in line with those of regional natural lakes (Kalff, 2002; Tremblay, 2004). There is evidence to suggest that the intensity of the trophic upsurge, as well as the amount of time which passes before a reservoir may produce CO_2 at the same rate as natural lakes, could be significantly related to the total carbon stock and carbon lability of a flooded landscape (Tremblay et al., 2004; Bodaly et al., 2004). In a highly heterogeneous region such as the boreal zone, CO_2 production in a large reservoir might therefore be expected to reflect each of the ecosystem types flooded. This has been observed in a study of two boreal reservoirs in northern Quebec, where benthic respiration rates were highest over flooded carbon-rich peatlands in young (two year old) and older (17 year old) reservoirs (Duchemin et al., 1995).

One of the first attempts to understand the specific responses of the boreal landscape to flooding was carried out in the Experimental Lakes Area in the boreal region of northern Ontario, Canada, and was called the Experimental Lakes Area Reservoir Project (ELARP) (Kelly et al., 1997). The ELARP reservoir flooded several hectares which encompassed a natural lake and peatlands, and examined the reservoir's production of GHGs for over a decade (Bodaly et al., 2004). From this study it became evident that these ecosystems were capable of releasing high quantities of GHGs over a long period of time (projected at possibly over 2000 years, Kelly et al., 1997). Furthermore, the expected pattern of a trophic upsurge followed by a decline was not apparent in this experimental reservoir, which may possibly

reflect the relatively small quantity of highly labile carbon typically found in the foliage of boreal forests (Matthews et al., 2005).

While the ELARP study was an important first step in understanding the specific response of lowland boreal ecosystem types to flooding, peatlands and natural aquatic environments compose the minority of landscape types flooded by large reservoirs such as Eastmain-1, whose benthic environment is instead mostly composed of flooded forests. In order to examine the impact of flooding on an uplands forest landscape, a set of three small experimental reservoirs were constructed as part of the Flooded Uplands Experiment (FLUDEX), also at the Experimental Lakes Area in northern Ontario. This project identified three types of forest based on their carbon stock, and flooded them in 1ha reservoirs with mean depths of 1 to 2m. Furthermore, bags containing various types of vegetative matter were submerged in the reservoir in order to measure the rate of decay in different types of vegetation. Finally, as reservoirs are frequently drawn down during the winter season, the FLUDEX reservoirs were drained each winter to replicate this effect (Matthews et al., 2005). It was predicted that the production of CO_2 in each reservoir would directly reflect the quantity of carbon in that ecosystem, yet it was instead discovered that all three experimental reservoirs produced similar quantities of carbon dioxide in the first years after inundation. Furthermore, unlike the lowlands ELARP reservoir, the FLUDEX reservoirs experienced a trophic surge in the first year after inundation, with GHG production rates falling and stabilizing again within several years. It was determined that differences in the proportions of highly labile carbon between sites resulted in similar flux values for the first years of the study (Matthews et al., 2005). This result differed significantly from the carbon-rich ELARP reservoir, which exhibited significantly higher CO_2 emissions than those in the FLUDEX reservoirs, and whose emissions did not peak until five to six years after inundation (Bodaly et al., 2004).

While both ELARP and FLUDEX are important and useful studies, neither can fully represent or be used to adequately predict the impact of a large hydroelectric

reservoir, which may experience localized currents, floods aquatic and terrestrial ecosystem types of a broad range of characteristics, transports nutrients over large areas, and which experiences periods of thermal stratification. Furthermore, by focusing primarily on the flooded benthic environment and surface fluxes, neither experimental reservoir study is able to accurately predict the impact of a flooded landscape on the water column of a large reservoir, despite studies showing that the oxidation of dissolved organic matter (DOM) in the water column of boreal reservoirs can be a significant source of CO_2 emissions (Lalonde, 2009). The present study is therefore an important step in linking past research projects with functional hydroelectric reservoirs.

An elephant in the room: Placing the metabolism of a young reservoir in the context of regional lakes

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Abstract

A young hydroelectric reservoir (Eastmain-1) in boreal Canada was compared to a group of thirteen regional lakes to identify differences in water column respiration rates as well as CO_2 accumulation rates in the hypolimnion during a thermally stratified period. Water column respiration rates were significantly higher in the reservoir than in natural lakes (with surface means of 61.4 ± 4.6 mg C m^{-3} d^{-1} in Eastmain-1 and 40.2 ± 3 mg C m^{-3} d^{-1} in lakes, and profundal means of 58.1 ± 11 mg C m^{-3} d^{-1} in Eastmain-1 and 17.6 ± 7.5 mg C m^{-3} d^{-1} in lakes). Hypolimnetic CO_2 accumulation rates were also higher in the reservoir than in natural lakes (with means of 78.8 ± 16 mg C m^{-3} d^{-1} in Eastmain-1 and 19.8 ± 2.7 mg C m^{-3} d^{-1} in lakes). Benthic respiration, estimated as the difference between hypolimnetic CO_2 accumulation and hypolimnetic water column respiration, was considerably more elevated in Eastmain-1 (334.5 ± 89.7 mg C m^{-2} d^{-1}) than in natural lakes (40.2 ± 8.4 mg C m^{-2} d^{-1}). Our findings further indicate that the mean relative contribution of benthic respiration towards total net CO_2 production during stratified periods was similar in both aquatic systems (23% in lakes, 26% in Eastmain-1). By placing a greater weight on the role of the water column in a reservoir's CO_2 production, this study provides evidence for a significant paradigm shift away from the common assumption that reservoir CO_2 emissions are predominantly the direct result of decaying vegetation in the benthic environment.

Key words: carbon cycling, climate change, hydroelectric reservoirs, boreal, CO_2 fluxes, lake metabolism

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Introduction

Rates of increase in atmospheric carbon dioxide (CO_2) over the past decade (1.9ppm/year) are the highest recorded since continuous direct measurements began in 1960 (IPCC, 2007). The associated climatic effects have driven researchers from a variety of fields to seek a better understanding of the transport and exchange pathways taken by greenhouse gases (GHGs) such as CO_2 and methane (CH_4) between terrestrial and atmospheric environments. Perhaps one of the most surprising discoveries has been the major role played by inland aquatic ecosystems such as lakes and streams, which have been found to sequester and/or release to the atmosphere over half of the carbon load they receive from terrestrial environments on their way to the oceans (Cole et al., 2007, Travik et al., 2009). While some artificial reservoirs may over time come to resemble natural aquatic system, all young reservoirs enhance atmospheric GHG fluxes both through the mineralization of stored terrestrial carbon pools as well as through the permanent removal of natural carbon sinks such as forests and peatlands (St. Louis et al., 2000). Recent estimates suggest that reservoirs likely represent nearly 10% of all land freshwater by surface area (Downing et al., 2006). Furthermore, artificial reservoirs may release the equivalent to as much as 7% of all estimated anthropogenic emissions on a 100 year time horizon (St. Louis et al., 2000). Despite the significant global role that these systems play in the natural and human landscapes, they remain poorly understood.

While methane is over 20 times more powerful than CO_2 as a GHG, most of it is generally oxidized near the flooded sediments (McGinnis et al., 2006), leaving CO_2 as the most significant GHG emitted by reservoirs (Duchemin et al., 1995). Surface CO_2 emissions from reservoirs exhibit a large degree of regional and temporal variability, yet follow notable trends across broad spatial scales. For instance, one study of 280 Canadian reservoirs suggested that aged boreal reservoirs in Quebec, Canada (>10 years old) generally have mean CO_2 surface fluxes over twice those of regional lakes, while reservoirs in British Columbia (western Canada) generally have

mean CO_2 surface fluxes of less than half those of regional lakes (Tremblay et al., 2004). In fact, some studies indicate that CO_2 surface fluxes of eastern Canadian reservoirs may be the highest in North America (Soumis et al., 2004). Beyond regional environmental variables such as light availability, precipitation, and air temperature, a significant portion of the variability in GHG emissions may be driven by the quantity and quality of organic carbon stored within the flooded vegetation and soils (Aberg et al., 2004). In short, the location of a given reservoir is likely to impact the quantity of CO_2 it releases to the atmosphere over its lifespan.

The boreal forests of Canada are home to many of its largest and most significant hydroelectricity generating projects. One of the largest biomes on Earth, the boreal zone spans northern Europe, Asia, and North America, and holds an estimated 25-37% of the global soil carbon pool (Venkiteswaran, 2002). In their natural state, boreal forests are generally considered CO_2 sinks while boreal peatlands may be considered GHG neutral with respect to the atmosphere (Roulet, 2000; St. Louis et al., 2000). Boreal lakes are a prominent feature of the landscape, transferring enough carbon to the atmosphere to possibly represent as much as 40% of the total annual CO_2 emissions of all natural lakes while only occupying roughly 20% of the world's total lake area (Algesten et al., 2003; Kortelainen et al., 2006). While many ecosystems such as tropical forests store the majority of their carbon in vegetation, most of the carbon in the boreal region is stored in the soils, with the result that boreal soils are considered to be several times higher in carbon density than their temperate or tropical counterparts (Malhi et al., 1999). Similarly, studies of carbon emissions from an experimentally flooded boreal peatland in northern Ontario have presented the possibility of long-lived (2000 years) elevated surface CO_2 emissions from such reservoirs (Kelly et al., 1997). Given the major role of the boreal zone in Canadian hydroelectricity production, a solid understanding of the metabolic characteristics and carbon budget of hydroelectric reservoirs in this environment is an important and essential step in any attempt to quantify and predict the extent of reservoir GHG emissions.

Estimates from a South American reservoir have indicated that as much as 39% of a reservoir's total CO_2 production may be degassed at the dam's outlet or lost at the river estuary, drawing into question the adequacy of relying on reservoir surface fluxes alone for estimates of total GHG emissions (Abril et al., 2005). Similar conclusions have been drawn from boreal hydroelectric reservoirs, where degassing at turbines can represent as much as 16% of a reservoir's total surface CO_2 emissions (Roehm and Tremblay, 2006). Reliable estimates of annual CO_2 emissions, as would be necessary for national GHG inventories, therefore demand a detailed and thorough understanding of all processes occurring within the reservoir. Given the large-scale decomposition of vegetation and peat following inundation, benthic respiration (defined in this study as any respiration occurring below the water column, including flooded soils or sediments as well as decomposing vegetation) is commonly assumed to be the dominant component of GHG emissions in northern reservoirs (Aberg et al., 2004). Such an assumption is reflected by the fact that many studies examining CO_2 production in reservoirs tend to focus on benthic respiration and surface emissions alone, without quantifying respiration within the water column (Duchemin et al., 1995; Venkiteswaran, 2002; Bodaly et al., 2004). Benthic respiration certainly plays a significant role in natural systems, as sediment bacterial populations may be two to three orders of magnitude higher than those in overlying waters, and natural lake sediments typically hold 1000 times the nutrients and carbon of the water column (den Heyer and Kalff, 1998; Pace and Prairie, 2005). Despite this, a large degree of variability exists in the relative contribution of the water column and benthic environment towards total respiration rates in natural and artificial aquatic systems (Vadeboncoeur et al., 2002). For instance, benthic respiration was found to represent only 20% of the total respiration in a tropical Brazilian reservoir (Abe et al., 2005), while a relative benthic contribution of up to 80% was reported in a Swedish boreal reservoir (Aberg et al., 2004). This reported range of variability is similar in natural lakes, as a mean benthic contribution of 15% was recorded in a group of lakes in subarctic Sweden (Aberg et al., 2007), and a benthic contribution of up to 50% was

estimated for a humic lake in Sweden (Jonsson et al., 2001). As it is clear that the relative contribution of benthic CO_2 production towards surface emissions varies between aquatic systems, the establishment of a regional standard for natural lakes is important in order to define the relationship between surface CO_2 emissions, the water column, and the benthic environment after a reservoir's inundation.

Direct measurements of benthic CO_2 production in reservoirs are often challenging because dense decomposing vegetation can obstruct the direct placement of benthic chambers on flooded soils. Because of this methodological constraint, and because local variability in sediment respiration rates within lakes is often large, estimates based on hypolimnetic CO_2 accumulation may lead to more accurate and integrative estimates of benthic respiration in a given system than a limited number of direct measurements (den Heyer and Kalff, 1998). In this context, we here present the results of a study which aims to quantify and compare water column and benthic CO_2 production in a recently flooded boreal reservoir by direct measurements of respiration in the water column and CO_2 accumulation in the hypolimnion. Our working hypothesis is that benthic respiration should play a more significant role in reservoirs than in natural lakes given the presence of a large decomposing carbon-rich substrate.

Materials and Methods

Study area

Commissioned at the end of 2005, Eastmain-1 (52'00N, 76'00W) is a young mesotrophic reservoir in central western Quebec, Canada (Figure 1). With a mean depth of 11.5m, a surface area of 603 km^2 and an installed capacity of 507MW, Eastmain-1 is a shallow, moderately sized reservoir compared to other hydropower schemes in Quebec (Hydro Quebec, 2009). Eastmain-1 overlies an ecologically heterogeneous, relatively low-lying region consisting primarily of wetlands, natural lakes, and forests, typical for boreal Canada and northern Europe. The particular area flooded by Eastmain-1 is composed of roughly 49% boreal forest, 18% peatlands, 25% natural aquatic systems, and 8% non-forest (bare) soils (Teodoru et al., submitted). The 13 sampled lakes surrounding Eastmain-1 are generally oligotrophic to mesotrophic with a mean Z_{mean} of 3.6m and a mean surface area of 0.5 km^2 (Table 1; Fig. 1). There are no significant adjacent or upstream human communities to the reservoir or sampled lakes.

Sampling

Sampling in the Eastmain-1 Reservoir was carried out at 11 sites, with each site consisting of two replicate stations. Sampling stations were designed so as to minimize any impact on the benthic environment while ensuring that the same spot within a radius of several meters could be sampled upon each visit. This was done by securing three anchors in a broad triangular formation with a boat tied in the center during sampling visits. Eastmain-1 sampling sites were distributed across the western, larger half of Eastmain-1 as it may be considered generally representative of the entire system in terms of the range of ecosystems which were flooded, while also experiencing low enough currents to allow for thermal stratification and reliable measurements of hypolimnetic CO_2 accumulation. The sampled natural lakes represent a cross-section of the range of bathymetric and biogeochemical characteristics prevalent in the region.

Both Eastmain-1 and the natural lakes were sampled three to six times from June to September, 2008. Each lake was visited three times over the single ice-free season. Reservoir sites were generally sampled once in June, three to four times during a one-week period in late July or early August, and once again in September. CO_2 surface fluxes were measured in replicate upon each visit using a floating chamber with a surface area of $0.1 m^2$, which created a closed circuit with an infrared gas analyzer (PPS Systems Environmental Gas Monitor, EGM-4 CO_2 analyzer). In accordance with methods described by Marchand et al. (2009), the partial pressure of CO_2 ($pCO2$) inside the chamber was recorded each minute for a period of 10 minutes. Linear regressions were used to compute the rate of accumulation within the chamber. Samplings were carried out near the geographical center of natural lakes in order to provide reliable estimates of lake pCO_2 levels for a given time period (Kelly et al., 2001). Due to the remoteness of this location, natural lakes were sampled by helicopter or hydroplane.

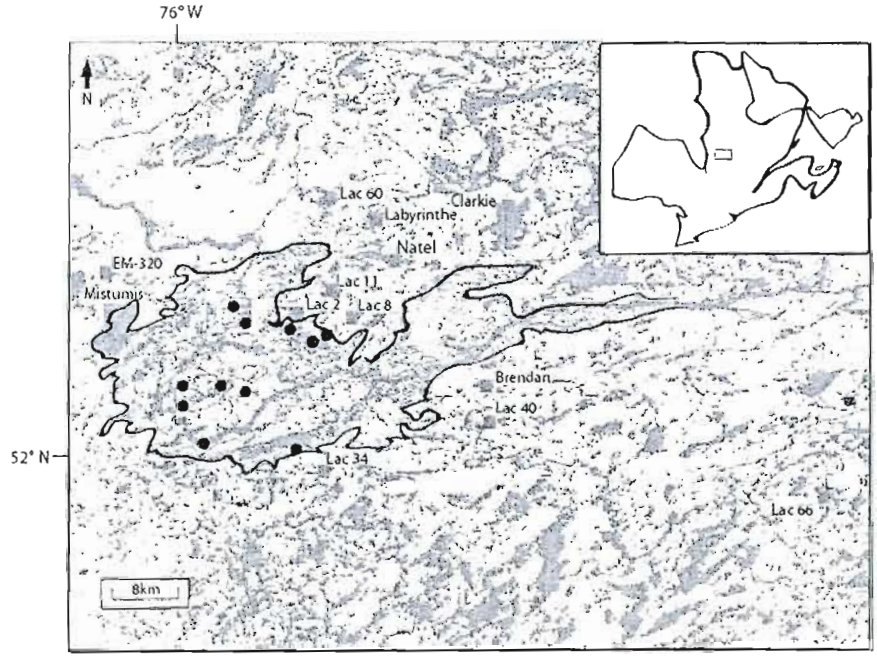
Vertical profiles of the water column were taken with a YSI environmental monitoring probe which recorded temperature, dissolved O_2 (mg L^{-1} and %), conductivity, and pH. The pCO_2 levels throughout the water column were measured *in situ* by pumping water with a peristaltic pump through a membrane equilibrator coupled to an infrared gas analyzer (EGM-4 CO_2 analyzer) in a closed circuit of gas flow (Cole and Prairie, 2009). The YSI probe was calibrated daily for O_2 and depth, with calibrations of pH and conductivity occurring three to four times over the sampling period. Profile measurements were recorded every 0.5 to 2m (in response to the rate by which conditions changed along the water column) from the surface to within 1 to 2m of the sediments (or the limit of our profiling equipment, 28m from the surface).

Along with profiles and surface flux measurements, top and bottom water samples were taken to measure dissolved organic and inorganic carbon (DOC, DIC), total nitrogen (TN), total phosphorus (TP), and water column respiration rates. DOC and DIC concentrations were measured from 0.2 μm-filtered water samples with a

Table 1. General characteristics of sampled lakes and Eastmain-1 Reservoir.

Name	Surface area (km^2)	Z_{mean} (m)	Volume (m^3)
Eastmain-1 Reservoir	603	11.5	6,940,000,000
Lac 2	0.04	1.5	58,592
Lac 8	0.3	2.6	782,443
Lac 11	0.36	1.6	582,265
Lac 34	0.45	4.5	2,049,436
Lac 40	0.16	4.5	718,249
Lac 60	1.35	5.7	7,762,697
Lac 66	0.07	4.1	286,476
Lac Brendan	1.04	3.8	3,969,126
Lac Clarkie	N/A	N/A	N/A
Lake EM-320	0.45	2.4	1,065,362
Labyrinthe	1.55	5	4,370,322
Mistumis	3.84	2.1	8,016,467
Natel	3.79	5.4	20,501,338
Mean of lakes	1.12	3.6	3,930,601

Figure 1. Map of the Eastmain-1 Reservoir (in light blue) showing the location of sampled lakes (represented by orange squares) and reservoir stations (black circles, each representing a pair of replicate stations).



Total Organic Carbon Analyzer (TOC) 1010-01 using wet persulfate oxidation, with a precision of 50 mg C m^{-3}. TN was measured as nitrates after alkaline persulfate digestion using an Alpkem Flow solution IV autoanalyzer. TP was measured with a spectrophotometer following potassium persulfate digestion with a precision of 5% (Murphy and Riley, 1962). Water column respiration rates were determined by calculating the mean rate at which O_2 was depleted in replicate water samples following methods outlined in Marchand et al. (2009). This was done by using a PreSense Systems Fibox oxygen meter, which measures the dissolved O_2 concentration of water samples in 500mL Erlenmeyer flasks using a non-intrusive fiber-optics sensor. Water samples, sealed with no airspace or bubbles, were stored in the dark so that no photosynthesis could occur. Epilimnetic samples were maintained at 17°C, while profundal water samples from thermally stratified sites were stored in coolers at approximately 10°C so as to minimize any change of temperature from the field to the laboratory. Oxygen levels were recorded every 12 hours beginning on the day which samples were collected, for a total of 60 hours. Epilimnetic water samples (considered in this paper as all surface water samples, whether or not a site is thermally stratified) were taken at a depth of 0.5m, and profundal water samples were generally taken from 1 to 2m above the sediments (as close to the bottom as possible without capturing sediments) up to 28m deep. Hypolimnetic samples are considered in this paper as any profundal samples taken during periods of thermal stratification.

Calculations

The overall CO_2 flux taken by floating chambers (F, mmol CO_2 m^{-2} d^{-1}) was determined by averaging replicates and using the formula:

(1) $$F = ((m \times V)/(V_m \times SA)) * 1.44$$

where m is the slope of augmentation of the CO_2 in the floating chamber (µatm min^{-1}), V is the volume of the floating chamber (L), V_m is a gas's molar volume (L*atm mol^{-1}), and SA is the surface area of water covered by the floating chamber (m^2). The

molar volume was calculated using the *in situ* barometric pressure measured by a Kestrel weather meter.

Measurements of water pCO_2 were converted to concentrations using Henry's constant for CO_2, correcting for the solubility of gases in water at different temperatures.

Primary production (PP) was estimated using del Giorgio and Peters' (1993) formula:

(2) $PP=10.3\ Chl^{1.19}$

where Chl is the concentration of chlorophyll *a* in a given water sample.

In thermally stratified sites, benthic respiration (BR) was calculated as:

(3) $BR = (\Delta C_{hypo} - WCR_{hypo}) * Z_{hypo}$

where ΔC_{hypo} is the hypolimnetic CO_2 accumulation rate as estimated from consecutive CO_2 profiles, WCR_{hypo} is the water column respiration rate in the hypolimnion, and Z_{hypo} is the hypolimnion thickness over which ΔC_{hypo} was calculated. The period of time used to calculate ΔC_{hypo} ranged from two days to approximately one month, according to the stability of stratification at a given site. Hypolimnetic CO_2 accumulation in natural lakes was volume-weighted for a greater accuracy of estimates. Our dependence upon hypolimnetic CO_2 accumulation rates for calculating benthic respiration requires the assumption that the vertical transfer of CO_2 across a stable thermocline is small relative to the rate of accumulation.

For each reservoir site or lake for which both benthic and water column respiration estimates were made, total net CO_2 production was estimated as:

(4) Total net CO_2 production $= (WCR_{epi} * Z_{epi}) + (WCR_{hypo} * Z_{hypo}) + BR - PP$

where Z_{epi} and Z_{hypo} are, respectively, the thickness of the epilimnion and hypolimnion. WCR_{epi} is the water column respiration rate in the epilimnion assuming a respiratory quotient of 1 (the mean value calculated in natural lakes and Eastmain-1, inferred from pCO_2, O_2, and temperature profiles).

All data were tested for normality, and logarithmic transformations were used when necessary to satisfy assumptions of normality where appropriate. All statistical tests were made using the computer program JMP (version 7, SAS Institute).

Results

Of 13 sampled lakes and 11 reservoir sites where water samples taken for laboratory analysis of water column respiration, profundal values from two lakes and two reservoir sites were poorly quantified or even exhibited a net positive accumulation of O_2 thereby yielding unreliable respiration rates. As we could not differentiate between natural phenomenon and methodological error these values were excluded from our analyses. In cases where reliable respiration rates were unavailable for a given lake during 2008, we used values at the same lake taken the previous year. No lakes displayed a significant difference between available hypolimnetic respiration rates across these two years, suggesting that the application of 2007 data to our 2008 dataset could be considered reasonably valid. Since no previous data were available for hypolimnetic water column respiration in the reservoir, 2008 mean reservoir values and values from neighboring sites were applied to reservoir sites for which reliable respiration rates were unavailable. As one lake (Lac 2) was too shallow to provide distinct surface and profundal water samples, measurements from this lake are here supplied as surface data alone.

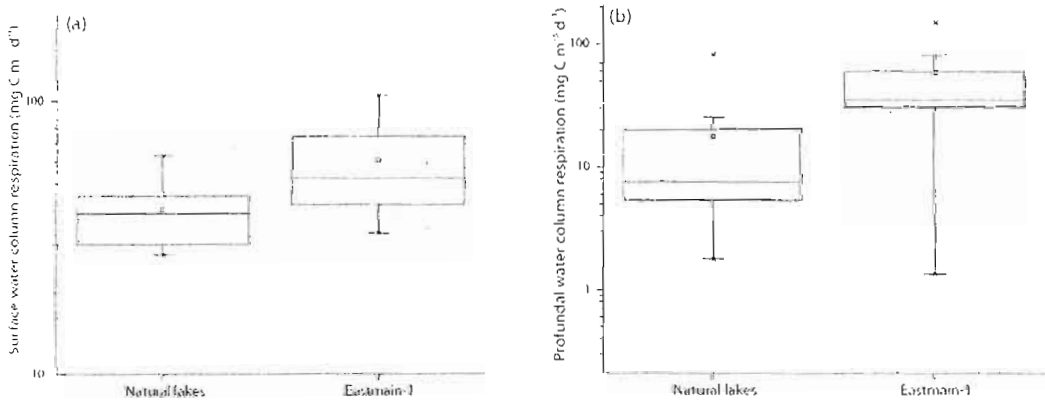
Seasonal mixing and stratification in Eastmain-1 and natural lakes followed the expected pattern for this region, with most sites thermally stratified early in the sampling season, and most mixed in September. Standard errors of the mean are provided for values given below.

Water column CO_2 production

Water column rates of CO_2 production are provided in Table 2. Epilimnetic water column respiration rates in natural lakes ranged from 22.5 to 102.6 mg C m^{-3} d^{-1} with a mean of 40.2 ± 3 mg C m^{-3} d^{-1}. Eastmain-1 epilimnetic water column respiration rates ranged from 32.8 to 115.6 mg C m^{-3} d^{-1} with a mean of 61.4 ± 4.6 mg C m^{-3} d^{-1}. Epilimnetic water column respiration rates were seasonally variable in both aquatic system types, generally declining from June to September. Profundal water column respiration rates in lakes ranged from 1.2 to 81.9 mg C m^{-3} d^{-1} with a mean of

17.6 ± 7.5 mg C m^{-3} d^{-1}. Eastmain-1 profundal water column respiration rates ranged from 1.4 to 149 mg C m^{-3} d^{-1} with a mean of 58.1 ± 11 mg C m^{-3} d^{-1}. Seasonality in profundal water column respiration rates was only apparent in natural lakes, where elevated rates were observed during the autumn overturn period. There was no significant difference between epilimnetic and profundal water column respiration in Eastmain-1, though epilimnetic water column respiration rates were significantly higher than profundal ones in natural lakes. Overall, epilimnetic and profundal respiration rates were significantly higher in Eastmain-1 than in natural lakes (Fig. 2).

Figure 2. (a) Surface (p = 0.0014, $\log_{10}$ transformations) and (b) profundal (p = 0.0036, $\log_{10}$ transformations) water column respiration rates in natural lakes and Eastmain-1.



CO_2 accumulation in the hypolimnion

Hypolimnetic CO_2 accumulation rates in natural lakes, ranging from 7.2 to 35 mg C m^{-3} d^{-1} (mean of 19.8 ± 2.7 mg C m^{-3} d^{-1}), were lower than those measured in Eastmain-1, which varied from 19.6 to 326.1 mg C m^{-3} d^{-1} (mean of 78.8 ± 16 mg C m^{-3} d^{-1}, Table 2). In fully stratified natural lakes a significant negative relationship was observed between changes in hypolimnetic DOC levels and changes in hypolimnetic pCO_2 levels, signaling the consumption of DOC in the hypolimnion over the sampling period (t-test, p = 0.008, one outlier excluded). Hypolimnetic DOC

levels in Eastmain-1 declined at a mean rate of 14.2 ± 34.3 mg C m^{-3} d^{-1}, which was an order of magnitude greater than the mean rate of decline observed in the hypolimnia of natural lakes (0.6 ± 4 mg C m^{-3} d^{-1}).

Benthic respiration

Derived from measurements of hypolimnetic CO_2 accumulation, estimates of benthic respiration in Eastmain-1 and natural lakes were limited to lakes and reservoir stations experiencing thermal stratification. Estimates of benthic respiration were available for eight lakes, and ranged from 13.5 to 109.6 mg C m^{-2} d^{-1} with a mean value of 40.2 ± 8.4 mg C m^{-2} d^{-1}. Estimates of benthic respiration in Eastmain-1 were available for 11 stations, and ranged between 11 and 1935 mg C m^{-2} d^{-1} with a mean value of 334.5 ± 89.7 mg C m^{-2} d^{-1} (Table 2; Fig. 3). Stations at which the accumulation of hypolimnetic CO_2 was less than could be explained by hypolimnetic water column respiration rates were excluded in order to minimize the possibility of including a station in which thermal stratification had been disturbed between sampling campaigns.

Whole-system metabolism and surface emissions

The total net CO_2 production, incorporating water column respiration (in the epilimnion and hypolimnion), benthic respiration, and primary production, had a mean value of 167.8 ± 16.8 mg C m^{-2} d^{-1} in natural lakes, which was significantly lower than the mean value of 1158 ± 138.7 mg C m^{-2} d^{-1} estimated for Eastmain-1 (Fig. 4). Benthic respiration was found to account for between 8 and 54% (mean 23%) of total net CO_2 production in natural lakes and 1 to 69% (mean 26%) of total net CO_2 production in Eastmain-1. Surface CO_2 emissions had a mean value of 471 ± 40.9 mg C m^{-2} d^{-1} in natural lakes, which was significantly lower than the mean value of 1343 ± 71.7 mg C m^{-2} d^{-1} for Eastmain-1.

Figure 3. Estimated benthic respiration rates in natural lakes and Eastmain-1 ($p < 0.0001$, $\log_{10}$ transformations).

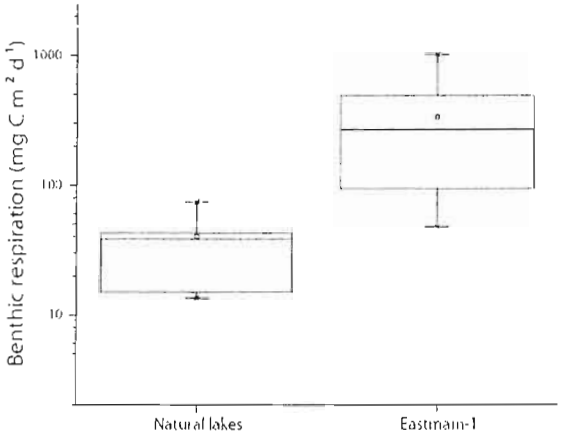


Figure 4. Total (benthic plus water column) CO_2 production rates in natural lakes and in Eastmain-1 showing estimated carbon-fixation by primary production, providing total net CO_2 production.

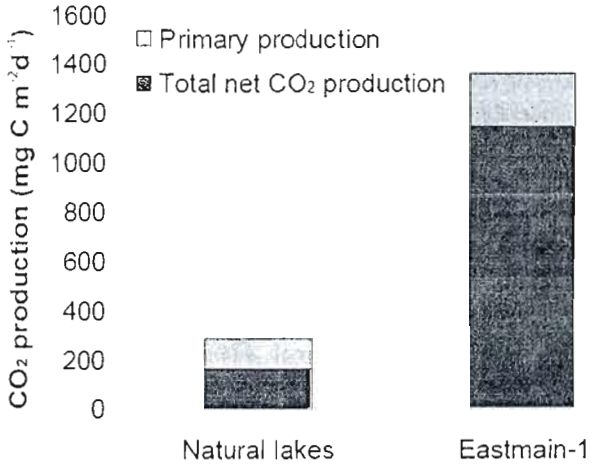


Table 2. Mean respiration, surface flux, and net CO_2 production values for natural lakes and Eastmain-1.

Name	Water column respiration rate (surface) (mg C m^{-3} d^{-1})	Water column respiration rate (profundal) (mg C m^{-3} d^{-1})	Hypolimnetic CO_2 accumulation (mg C m^{-3} d^{-1})	CO_2 surface flux (mg C m^{-2} d^{-1})	Benthic respiration rate (mg C m^{-3} d^{-1})	Total net CO_2 production (mg C m^{-2} d^{-1})	Mean contribution of benthic respiration towards total net CO_2 production (%)
Eastmain-1 Reservoir*	61.4 ± 4.6 (n = 22)	58.1 ± 11 (n = 16)	78.8 ± 16 (n = 15)	1343 ± 71.7 (n = 22)	334.5 ± 89.7 (n = 11)	1158 ± 138.7 (n = 11)	26 ± 5 (n = 11)
Lac 2	63.3 ± 9.4 (n = 3)	-----	-----	283.6 ± 170.5 (n = 3)	-----	-----	-----
Lac 8	35.2 ± 7.7 (n = 3)	81.9 (n = 1)	30.8 (n = 1)	426.5 ± 160.6 (n = 3)	46.2 (n = 1)	194.5 (n = 1)	22 (n = 1)
Lac 11	56.7 ± 23 (n = 3)	12.2 ± 1.8 (n = 2)	-----	490.7 ± 46.7 (n = 3)	-----	-----	-----
Lac 34	38.8 ± 2.3 (n = 3)	1.8 (n = 1)	21 (n = 1)	525 ± 31.4 (n = 3)	38.4 (n = 1)	120.1 (n = 1)	32 (n = 1)
Lac 40	39.4 ± 7.6 (n = 3)	-----	21.2 (n = 1)	421.6 ± 22.8 (n = 3)	21.6 (n = 1)	158.3 (n = 1)	14 (n = 1)
Lac 60	29.7 ± 2.7 (n = 3)	2.2 ± 1 (n = 2)	7.2 (n = 1)	329 ± 196.7 (n = 3)	15 (n = 1)	87.7 (n = 1)	17 (n = 1)
Lac 66	45.2 ± 5 (n = 3)	7.6 (n = 1)	31.3 ± 3.8 (n = 2)	583.1 ± 95.6 (n = 3)	74.6 ± 34.9 (n = 2)	164.2 ± 36.8 (n = 2)	43 ± 12 (n = 2)
Lac Brendan	37.8 ± 0.9 (n = 2)	20.2 (n = 1)	13.2 (n = 1)	325 ± 86.2 (n = 3)	-----	-----	-----
Lac Clarkie	27.4 ± 1.9 (n = 3)	12.4 ± 3.8 (n = 2)	-----	391.7 ± 249.3 (n = 2)	-----	-----	-----
Lake EM-320	46.5 ± 11.2 (n = 3)	7 ± 0.7 (n = 2)	-----	852.2 ± 66.3 (n = 3)	-----	-----	-----
Labyrinthe	29 ± 3.4 (n = 3)	25.4 ± 19.1 (n = 2)	21.4 ± 0.4 (n = 2)	479.4 ± 133.6 (n = 3)	73.4 (n = 1)	223.9 (n = 1)	33 (n = 1)
Misnumis	44.1 ± 10.8 (n = 3)	5.4 (n = 1)	12.1 (n = 1)	577.2 ± 125.4 (n = 3)	13.5 (n = 1)	169.7 (n = 1)	8 (n = 1)
Natel	29.8 ± 4.1 (n = 3)	-----	20 (n = 1)	37.4 ± 47.5 (n = 3)	42.4 (n = 1)	223.8 (n = 1)	19 (n = 1)
Lake means	40.2 ± 3 (n = 13)	17.6 ± 7.5 (n = 10)	19.8 ± 2.7 (n = 9)	471 ± 40.9 (n = 13)	40.2 ± 8.4 (n = 8)	167.8 ± 16.8 (n = 8)	23 ± 4 (n = 8)

* Station means used

Discussion

Comparison with previous studies

Epilimnetic respiration rates in our sampled boreal lakes were generally lower than those estimated for north-temperate lakes at equivalent phosphorus levels (roughly 60 to 200 mg C m^{-3} d^{-1}; Pace and Prairie, 2005), while profundal respiration rates of 6.0 to 72.1 mg C m^{-3} d^{-1} in southern Quebec lakes were comparable to our own (Cornett and Rigler, 1987).

Estimated benthic CO_2 production rates in our sampled natural lakes were comparable to those of Algesten et al. (2005), who calculated benthic CO_2 production rates ranging from -53 to 182 mg C m^{-2} d^{-1} in a group of 15 boreal and subarctic European lakes. Similarly, Pace and Prairie (2005) expresses the relationship between benthic respiration rates and total phosphorus levels in natural lakes with the equation:

(5) $\log_{10} BR_{std\ 10°C} = 0.17 + (0.58)(\log_{10} TP)$

with benthic respiration (BR) in mmoles O_2 m^{-2} d^{-1} and total phosphorus (TP) in mg m^{-3}. Applying this relation to our dataset (which had a mean benthic temperature of roughly 10°C) would predict a mean lake benthic respiration rate in the vicinity of 64.7 mg C m^{-2} d^{-1}, a value reasonably close to our estimated mean benthic respiration rate in lakes (40 mg C m^{-2} d^{-1}). However, given higher phosphorus levels in Eastmain-1 (which also had a mean benthic temperature of roughly 10°C), their equation would predict reservoir benthic respiration rates of 83 mg C m^{-2} d^{-1}, which is far lower than our estimated value for the reservoir (360 mg C m^{-2} d^{-1}). Eastmain-1 therefore did not fall within the range of benthic respiration rates observed in natural systems for the period studied. Plankton-derived POC is primarily driven by total phosphorus (Smith and Prairie, 2004), suggesting that the observed difference between system-types may possibly represent a larger role for allochthonous DOC in benthic respiration in the reservoir than in natural lakes. Our estimates of benthic respiration in Eastmain-1 were generally within the range of those estimated for two other Quebec reservoirs (102 to 1825 mg C m^{-2} d^{-1}), as measured by benthic

chambers in reservoirs that were two years old and 17 years old at the time of the study (Duchemin et al., 1995).

The ratio of water column CO_2 production in the epilimnion and hypolimnion of our sampled lakes and reservoir appeared to be within the range reported by Cornett and Rigler (1987), which found water column respiration rates in the hypolimnion to represent 15 to 66% of the total water column production. Examining the relative contribution of the benthic environment towards surface CO_2 emissions, our findings (23% in lakes, 26% in Eastmain-1) resemble those of Jonsson et al. (2001), who found benthic respiration in a Swedish boreal lake to represent roughly 30 to 50% of the total C production.

In comparison with studies carried out in the boreal regions of northern Europe, it is evident that our natural lakes, as well as the reservoir, fall within a previously expressed range of variability. This indicates an existing homogeneity between these similar but broadly situated environments.

Comparison of CO_2 production in Eastmain-1 and lakes

The role of benthic respiration in natural lakes is often a function of morphometry as well as trophic status (den Heyer and Kalff, 1998). High benthic respiration rates in Eastmain-1 instead indicate the strong influence of the flooded environment, rich in organic carbon and nutrients. The impact of the flooded terrestrial environments extends above the benthic environment itself, however, as is reflected in the reservoir's comparatively high total phosphorus levels (14.2 ± 0.4 μg L^{-1} in Eastmain-1, compared to 9.3 ± 0.8 μg L^{-1} in surrounding lakes and a mean of 9.0 μg L^{-1} in the Eastmain River (Teodoru et al., 2009)). These elevated nutrient levels are frequently associated with high rates of DOC consumption (Smith and Prairie, 2004), which could explain the more rapid loss of DOC observed in the water column of the reservoir. While this study focuses on metabolic processes in the water column, other studies have reported higher levels of photomineralization in boreal reservoirs than in natural lakes, suggesting that the water column of Eastmain-1 may

in fact be a larger source of CO_2 than indicated by this study (Soumis et al., 2007). Further evidence towards the influence of the benthic environment on water column respiration rates may be evidenced by the similarities between mean profundal (58.1 ± 11 mg C m^{-3} d^{-1}) and epilimnetic (61.4 ± 4.6 mg C m^{-3} d^{-1}) water column respiration rates in Eastmain-1, despite generally lower associated water temperatures at greater depths. Our findings not only suggest that the release of CO_2 in Eastmain-1 is predominantly from respiration within the water column, but that the flooded terrestrial environments may have influenced this distribution of CO_2 production. This is in accordance with a previous studies which have found that dissolved organic matter (DOM) in boreal reservoirs is generally terrestrial in origin, and that its oxidation in the water column can be a significant source of CO_2 surface emissions (Lalonde, 2009).

Relationship between CO_2 production estimates and surface fluxes

Estimates of net CO_2 production in natural lakes and the Eastmain-1 Reservoir follow a single, significant linear relationship with measured surface CO_2 fluxes from the same time periods, lending support to our estimates of the individual compartments of CO_2 production in these aquatic systems (Fig. 5). Separating these two aquatic system types, estimates of net CO_2 production in Eastmain-1 were in the same range as, and significantly positively related to, surface CO_2 fluxes taken by floating chambers over the same time periods (t-test, $p = 0.003$), while estimates of net CO_2 production in natural lakes were less than half of the mean measured surface CO_2 fluxes taken over the same time period, and no significant relationship existed between them. The difference in magnitude between measured and estimated CO_2 fluxes observed in natural lakes may be partly due to the tendency of floating chambers to significantly overestimate surface fluxes, especially under low-turbulence conditions which would be more prevalent in small lakes than in Eastmain-1 (Vachon et al., submitted). Furthermore, stratification tended to be stronger and more persistent in lakes than in Eastmain-1, and the benthic CO_2

production would tend to accumulate in the hypolimnion of lakes more than in the reservoir, thus contributing less to the surface CO_2 fluxes of lakes during periods of stratification. The lack of a significant relationship between estimated net CO_2 production and surface fluxes in natural lakes appears to be largely a product of a diminished range of variables, though it may also reflect a larger proportional input of stream inputs (Dillon and Molot, 1997) or benthic respiration from the littoral zones of lakes, which are considered important locations for the production of GHGs (Huttunen et al., 2003; den Heyer and Kalff, 1998).

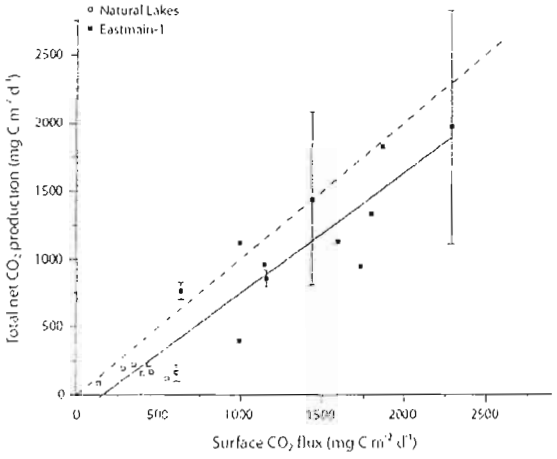
Spatial variability of benthic respiration in Eastmain-1 and natural lakes

Given the limited duration of the boreal ice-free period (roughly five to six months), our measurements may be seen as representing only a small portion of the full picture of metabolic processes in Eastmain-1 and regional lakes. In a parallel study, we have concluded that winter under-ice accumulation represents on average 30% of the total annual CO_2 budget in these same lakes (Ducharme Riel et al., in preparation). Furthermore, it was established that approximately 40 to 80% of the total winter CO_2 accumulation was due to benthic respiration (Ducharme Riel, unpublished), suggesting that the role of the water column is much diminished during the winter in these lakes, and presumably in the reservoir as well.

As our estimates of benthic respiration are derived from our measurements of CO_2 accumulation in the hypolimnion, our results can only be directly applied to the stratified periods of both system types. These conclusions are therefore subject to a potential bias towards deeper, more stratified sites. Within Eastmain-1, this may be expressed by a negative relationship between site depth and the contribution of benthic respiration towards the total net CO_2 production. Sampled natural lakes did not vary as widely in depth as the sampled reservoir sites, though they generally fell within the same such relationship seen in the reservoir. This suggests that the proportional contribution of the water column and benthic environment towards total

CO_2 production may in fact be determined more by morphometry than by the nature of an aquatic system itself.

Figure 5. Estimated total net CO_2 production by measured surface CO_2 flux (station/lake means; t-test, $r^2 = 0.86$, $p < 0.0001$). Error bars represent the standard error of the mean for sites where more than one estimate of total net CO_2 production was available.



Conclusions

We had predicted that benthic respiration would play a more significant role in Eastmain-1 than in surrounding natural lakes, yet both systems were found to be similar in regards to the proportional contributions of benthic and water column CO_2 production towards total CO_2 production. Flooded terrestrial environments not only emit larger quantities of CO_2 than natural lake sediments, but they also appear to provide the water column with DOC and nutrients which are associated with elevated respiration rates in the water column. As a result, the relative contribution of each source of respiration appears to depend more upon the mean depth of a system than the type of aquatic system.

Further studies are required in order to determine whether our observed ratio between benthic and water column respiration might vary with a reservoir's age. Regardless, it is the flooded benthic environment which shapes the metabolism in

Eastmain-1, and inter-annual variations in reservoir CO_2 production are likely to be related to the specific types of flooded landscapes present. For example, Duchemin et al. (1995) reported differing benthic respiration rates based on the type of landscape (ie. forest, peatland, etc.) which had been flooded by two boreal Quebec reservoirs. The flooded landscape-type may also influence the longevity of benthic fluxes, as suggested by Kelly et al. (1997), with carbon-rich landscape-types such as peatlands having a long-term potential for elevated rates of decomposition (>2000 years) due to their high content of organic carbon.

Our study has identified the role of the benthic environment in a boreal reservoir in relation to natural lakes, placing the metabolic characteristics of a young boreal reservoir into a regional as well as a global context. Still, many facets of reservoir metabolism remain unsolved. Given this, coupled with the prevalence of reservoirs and future potential for their continued construction, it is time for researchers to begin asking (and answering) questions about this elephant in the room.

Reconstructing a flux: Landscape heterogeneity influences CO_2 production in a young boreal reservoir

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Abstract

Landscape-derived heterogeneity of CO_2 production within and between reservoirs has been examined in several studies over the past decades, though no quantitative link has yet been made between surface CO_2 emissions and the underlying flooded landscape. One possible source for this could be a lack of any comprehensive analysis of the effect that a flooded landscape has on CO_2 production in the water column and benthic environment of a reservoir. Recent research suggests that the water column is often a major contributor of CO_2 towards reservoir surface emissions, and that it can exhibit a spatial heterogeneity reflective of the flooded landscape below. The present study advances such previous research by uniting landscape-derived heterogeneity in the water column with heterogeneity in the benthic respiration rates of a young boreal reservoir (Eastmain-1) in Quebec, Canada. This study finds that the nature of a flooded landscape can have a significant influence on benthic respiration and the release of terrestrial dissolved organic carbon into the water column, ultimately influencing water column respiration rates as well as surface CO_2 emissions. In particular, CO_2 production in the reservoir was found to be positively related to the carbon stock of a flooded landscape, as measured prior to the reservoir's inundation or in corresponding regional landscapes. As our measured reservoir surface CO_2 emissions corresponded with our independently-derived estimates of CO_2 production within the system, this study presents an opportunity for increasingly accurate estimates of greenhouse gas (GHG) emissions from reservoirs prior to their construction.

Key words: carbon cycling, climate change, hydroelectric reservoirs, boreal, CO_2 fluxes, lake metabolism

Acknowledgments

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Introduction

The creation of large impoundments, converting predominantly terrestrial landscapes to aquatic ones, constitutes one of the most extreme examples of ecosystem transformation on Earth yet such reservoirs remain under-represented in the limnological literature. While early studies focused on the social or ecological impacts of these systems (Rosenberg et al., 1995; Tremblay et al., 1998), reservoirs also provide a unique opportunity to better understand the complex processes governing the transport, exchange, and transformation of carbon between the terrestrial, aquatic, and atmospheric environments. With clear implications for global climate change, the transport of carbon from a reservoir into the atmosphere in the form of GHGs such as carbon dioxide (CO_2) or methane (CH_4) is not negligible (Kelly et al., 1997; Matthews et al., 2005; Tranvik et al., 2009). CO_2 is considered of particular importance in these systems, as the majority of CH_4 produced is frequently oxidized before reaching the atmosphere (Duchemin et al., 1995; Abe et al., 2005). Although several studies suggest an important role for the flooded landscape in influencing benthic and surface CO_2 emissions, this relationship has not yet been fully quantified (Rosenberg et al., 1997; Matthews et al., 2005). In many cases, this may be due to the frequent exclusion of CO_2 production located within the reservoir's water column from such studies despite evidence suggesting that a reservoir's water column can be an important source of CO_2 emissions (Abe et al., 2005; Lalonde, 2009; Brothers et al., submitted). Furthermore, a recent study on a young hydroelectric reservoir in northern Quebec (Eastmain-1) observed a significant relationship between water column respiration rates and underlying flooded landscapes, suggesting the possibility of a landscape-derived heterogeneity at all levels of CO_2 production in the reservoir (Teodoru et al., submitted). Coupled with research which has linked inundation with significant increases in the concentration of nutrients and dissolved organic carbon (DOC) in a reservoir's water column (Paterson et al., 1997), it appears likely that a flooded landscape might influence surface CO_2 emissions not only by direct decomposition located at the benthic level,

but also indirectly by altering the water column above it. The present study addresses this topic by independently examining the spatially heterogeneous character of CO_2 production in the Eastmain-1 Reservoir, and places it in the context of the underlying landscape prior to inundation.

Occupying roughly 14.3 million km^2 of northern Europe, Asia, and North America (Venkiteswaran, 2002), the boreal zone is a highly heterogeneous landscape and is the location of much of Canada's hydroelectric production. A reservoir the size of Eastmain-1 (603 km^2), considered average compared to other hydropower schemes in Quebec, generally floods multiple forest-types as well as peatlands, natural lakes, streams, and the original river channel. Boreal forests are generally dominated by coniferous trees, though the presence of deciduous patches and frequent forest fires (which burn roughly 1% of North America's boreal forests annually) create distinct upland landscapes with differences in areal carbon stocks (Marchand et al., 2009). Boreal peatlands, typically located at lower elevations, are rich in carbon (~ 113 kg C m^{-2}), and after inundation are often limited to the deeper or intermediate waters in a reservoir (Roulet, 2000; Horwath, 2008). Flooded forests, relatively poor in carbon stock in comparison with peatlands (~ 5 to 8 kg C m^{-2}, Kortelainen et al., 2004; Banville et al., submitted), are often positioned across warmer, shallower epilimnetic waters during the ice-free period. Flooded aquatic ecosystems, represented primarily by lakes and the original riverbed, are typified by relatively low sediment respiration rates, and are generally located at the deepest areas of a reservoir. While river sediments typically have very low carbon stocks (~ 0.1 kg C m^{-2}, Jonsson et al., 2007), lake sediments are often comparatively rich in carbon (~ 15 to 20 kg C m^{-2}, Kortelainen et al., 2004; Teodoru et al., submitted). The differences in elevation between landscapes can also have potential implications during the winter draw-down period of a reservoir, exposing shallow forested sections to annual dry periods (Matthews et al., 2005). Given the high level of landscape heterogeneity, and the large discrete differences in carbon stock over a relatively small area, the boreal

environment provides an excellent opportunity for researchers to examine the relationship between landscape and reservoir CO_2 production.

As reservoirs will continue to be constructed for a wide range of purposes, a method of estimating their carbon emissions prior to inundation is sorely needed. The establishment of such a method requires the comparison of GHG production within a reservoir with the terrestrial and natural aquatic ecosystems which it has replaced. Such a comparison was carried out in two small-scale experimental reservoir studies, the Experimental Lakes Area Research Project (ELARP) and the Flooded Uplands Experiment (FLUDEX) (Kelly et al., 1997; Matthews et al., 2005). These experiments, both carried out in the boreal zone of northern Ontario, found that variable carbon lability could lead to uniform CO_2 production rates in the first three years after inundation between forested sites of differing carbon stock (Matthews et al., 2005). Furthermore, CO_2 production was found to decline rapidly after an initial peak in forest-dominated reservoirs, while a peatlands and lake-dominated reservoir did not reach peak levels of CO_2 emissions until five to six years after flooding (Bodaly et al., 2004). Over time, therefore, the lowland carbon-rich reservoir expressed both a longer potential duration of elevated CO_2 emissions, as well as much higher intensity of CO_2 fluxes in general. This implies that the quantity of carbon in a flooded landscape may significantly influence a reservoir's export of CO_2 over its lifespan. While such experimental reservoirs are useful tools in understanding the response of various benthic environments to flooding, their shallow nature and the general lack of water column respiration measurements from these studies makes it difficult to directly apply their findings to observed surface CO_2 emissions in hydroelectric reservoirs. Prior research on the heterogeneity of surface CO_2 emissions and water column respiration in the Eastmain-1 Reservoir has shown a clear relationship between flooded landscapes and CO_2 production rates, yet the hypolimnetic environment (including benthic respiration rates) has not been directly considered, making a link between surface CO_2 emissions and processes at the benthic level difficult to establish (Teodoru et al., submitted). The objective of the

present study is to examine heterogeneity in the benthic and water column metabolism of a newly created hydroelectric reservoir in relation to the heterogeneity in landscapes prior to flooding. Our working hypothesis is that significant differences in the carbon stock of a given landscape have direct and quantifiable impacts upon the carbon transformations occurring in the benthic environment, the water column, and surface CO_2 emissions of a young boreal reservoir.

Materials and Methods

Study area

The Eastmain-1 Reservoir (52'00N, 76'00W), commissioned in 2005, is a currently mesotrophic hydroelectric reservoir located in northern Quebec, Canada (Figure 1). With an installed capacity of 507MW, Eastmain-1 is a shallow (Z_{mean} = 11.5m), moderately sized reservoir compared to other hydropower schemes in Quebec (Hydro Quebec, 2009). The area flooded by Eastmain-1 is composed of roughly 49% boreal forest, 18% peatlands, 25% natural aquatic systems, and 8% non-forest (bare) soils (Teodoru et al., submitted). Being the first full-scale reservoir to be studied before and after flooding, information on the carbon content and natural terrestrial respiration in the regions flooded is available for the present study (Table 1).

Sampling

Sampling in Eastmain-1 was carried out at 11 sites, each consisting of two stations (providing replicate data). Each station was designed so as to minimize any impact on the benthic environment while ensuring that the same area within several meters would be repeatedly sampled. Stations were established by installing three anchors in a broad triangular formation so that a sampling vessel could be secured in the center with each visit. Sampling sites were distributed across the western, larger half of Eastmain-1 as it is generally representational of the range of flooded landscapes within the ecosystem, yet also experienced low enough currents to allow for thermal stratification and reliable measurements of hypolimnetic CO_2 accumulation (from which estimates of benthic respiration could be derived). Each site was chosen to represent a distinct flooded landscape type whose location was determined from extensive regional mapping prior to the reservoir's inundation. Flooded peatlands, lakes, riverbed, mature forest, and 17 year old burned forests were each represented by two sites in different regions of the reservoir, while only one site was possible for two year old burned forests in the reservoir. Mean carbon stock and

pre-inundation sediment and soil respiration values for these landscapes are provided in Table 1. Replicate stations at each site were generally located one to two hundred metres apart, depending upon the extent of the underlying landscape.

Figure 1. Map of the western portion of the Eastmain-1 Reservoir, showing flooded landscapes and the location of sampled sites (black circles, each representing two stations).

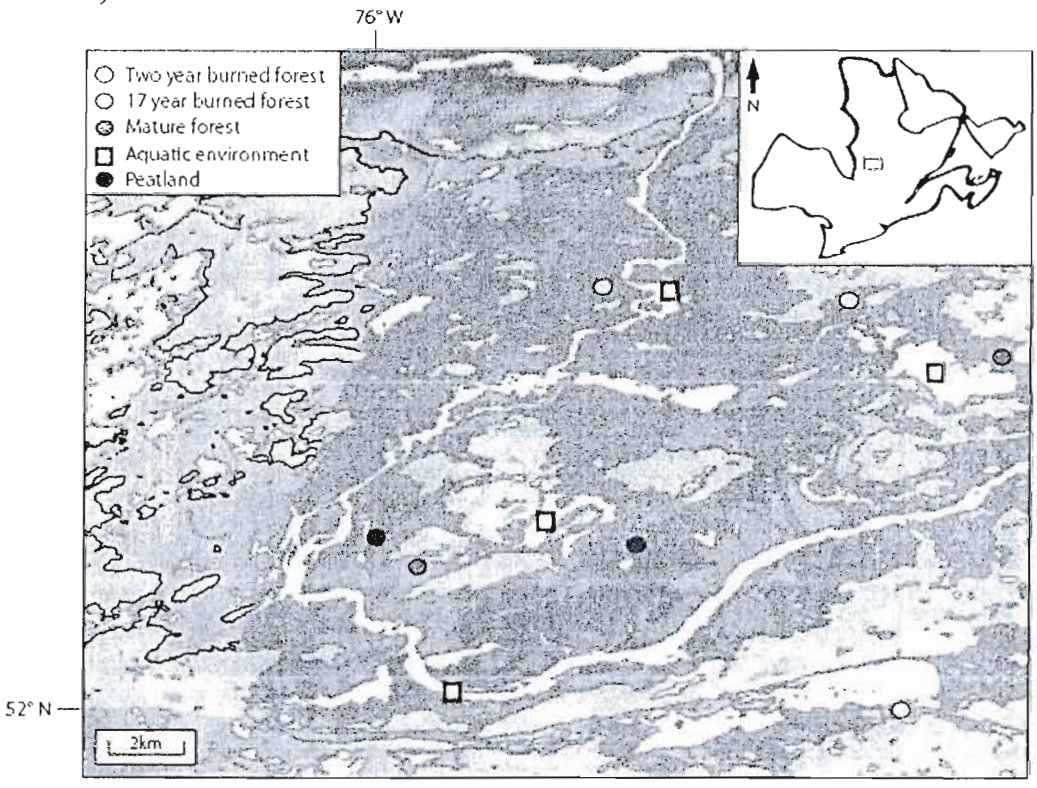


Table 1. Pre-inundation landscape characteristics.

Flooded landscape type	Pre-inundation soil carbon stock (kg C m^{-2})	Pre-inundation sediment respiration (mg C m^{-2} d^{-1})	Flooded area (km^2)
Eastmain River channel	0.1	68.5	83.2
Two year burned forest	5.8	243.2	6.1
17 year burned forest	6.1	332.2	107.7
Mature forest	7.6	244.9	164
Mean of forest landscapes	6.5	273.4	-----
Lakes	15.2	40.1[T]	66.9
Peatlands	112.8	634.1	110.9
Eastmain-1 mean	6.5*	304*	603 (total)

* Weighted by flooded landscape surface area

Note. The remaining 11% of reservoir area not in this table are shared by non-forest (bare) soils and deciduous forests

All data derived from Teodoru, C.R., Prairie, Y.T., and del Giorgio, P.A. Submitted to Environ. Sci. Technol., except [T], which is derived from Brothers, S.M., Prairie, Y.T., and del Giorgio, P.A. Submitted to Global Biogeochem. Cycles. Pre-inundation soil respiration rates for terrestrial landscapes are estimated as 50% of ecosystem respiration rates (based on mean values provided in Roehm, 2005).

Each station was visited four to six times from June to September, 2008, being generally sampled once in June, three to four times during a one-week period in late July or early August, and once again in September. This sampling schedule was adopted so that changes at a given site would be recorded on a large time scale (over a period of a month), as well as a small one (over a period of several days to a week). CO_2 surface fluxes were measured in replicate upon each visit using a floating chamber with a surface area of 0.1 m^2, with which a closed circuit was established with an infrared gas analyzer (PPS Systems Environmental Gas Monitor, EGM-4 CO_2 analyzer). In accordance with methods described by Marchand et al. (2009), the partial pressure of CO_2 inside the chamber was recorded each minute for a period of 10 minutes. Linear regressions were used to compute the rate of accumulation within the chamber.

Vertical profiles of the water column were taken with a YSI environmental monitoring probe, which recorded temperature, dissolved O_2 (mg L^{-1} and %), conductivity, and pH. The partial pressure of carbon dioxide (pCO_2) throughout the

water column was measured *in situ* by pumping water by peristaltic pump through a membrane equilibrator coupled to an infrared gas analyzer (EGM-4 CO_2 analyzer) in a closed circuit of gas flow (Cole and Prairie, 2009). The YSI probe was calibrated daily for O_2 and depth, with calibrations of pH and conductivity occurring three to four times over the sampling period. Vertical profile measurements were taken at intervals of 0.5 to 2m (varying with the rate at which conditions changed along the water column) from the surface to within 1 to 2m of the sediments (or the limit of our profiling equipment, 28m from the surface).

Surface and bottom water samples were taken at each station to measure dissolved organic and inorganic carbon (DOC, DIC) and water column respiration rates. DOC and DIC concentrations were measured from 0.2 µm-filtered water samples with a Total Organic Carbon Analyzer (TOC) 1010-01 using wet persulfate oxidation, with a precision of 50 mg C m^{-3}. Water column respiration rates were determined by calculating the rate at which O_2 was depleted in replicate water samples following methods outlined in Marchand et al. (2009). This was done with a PreSense Systems Fibox oxygen meter, which measures the dissolved O_2 concentration of water samples in 500mL Erlenmeyer flasks using a non-intrusive fiber-optics sensor. Water samples, sealed without airspace or bubbles, were kept in the dark so that no photosynthesis could occur. Epilimnetic samples were maintained at 17°C, while hypolimnetic water samples were maintained at approximately 10°C so as to minimize any change of temperature between the field and laboratory. O_2 levels were recorded every 12 hours over a 60 hour period, beginning on the day which samples were collected. Epilimnetic water samples (referred to here as any surface water samples, regardless of thermal stratification at a site) were taken at a depth of 0.5m, and profundal water samples were generally taken at 1 or 2m from the sediments (as close to the bottom as possible without capturing sediments) to a maximum depth of 28m. The methods used to analyse water column respiration rates in this study are consistent with those carried out in all other years of study at Eastmain-1.

Calculations

CO_2 emissions measured by floating chambers (F, mmol CO_2 m^{-2} d^{-1}) were calculated by averaging replicates and using the formula:

(1) $F = ((m \times V)/(V_m \times SA)) * 1.44$

where m is the slope of augmentation of the CO_2 in the floating chamber (μatm min^{-1}), V is the volume of the floating chamber (L), V_m is a gas's molar volume (L*atm mol^{-1}), and SA is the surface area of water under the floating chamber ($0.1 m^2$). The molar volume was calculated using the *in situ* barometric pressure, measured by a Kestrel weather meter.

Measurements of water pCO_2 were converted to concentrations using Henry's constant for CO_2, correcting for the solubility of gases in water at different temperatures.

Primary production (PP) was estimated using del Giorgio and Peters' (1993) formula:

(2) $PP=10.3\ Chl^{1.19}$

where Chl is the concentration of chlorophyll *a* in a given water sample.

Benthic respiration (BR) was estimated for thermally stratified sites as:

(3) $BR = (\Delta C_{hypo} - WCR_{hypo}) * Z_{hypo}$

where ΔC_{hypo} is the hypolimnetic CO_2 accumulation rate as estimated from CO_2 profiles, WCR_{hypo} is the water column respiration rate in the hypolimnion, and Z_{hypo} is the hypolimnion thickness over which ΔC_{hypo} was calculated. The period of time used to calculate ΔC_{hypo} ranged from two days to approximately one month, depending on the stability of stratification at a given site. Our dependence upon hypolimnetic CO_2 accumulation rates for calculating benthic respiration assumes that the vertical transfer of CO_2 across a stable thermocline is small relative to the rate of accumulation.

Total net CO_2 production was estimated as:

(4) Total net CO_2 production $= (WCR_{epi} * Z_{epi}) + (WCR_{hypo} * Z_{hypo}) + BR - PP$

where Z_{epi} and Z_{hypo} are, respectively, the thickness of the epilimnion and hypolimnion. WCR_{epi} is the water column respiration rate in the epilimnion assuming a respiratory quotient (RQ) of 1 (the mean value calculated in Eastmain-1 from pCO_2, O_2, and temperature profiles). RQ slopes and intercept values in this study were taken from a model 2 equal variance linear regression.

All data were tested for normality, and logarithmic transformations were used when necessary to satisfy assumptions of normality where appropriate. All statistical tests were made using the computer program JMP (version 7, SAS Institute).

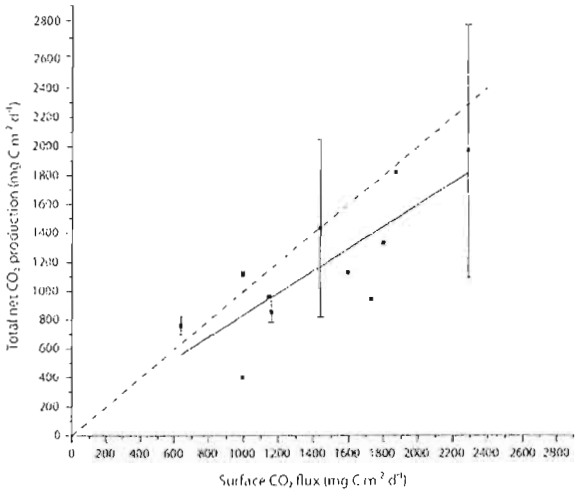
Results

Of 11 reservoir sites where water samples were taken for laboratory analysis of water column respiration, profundal values from two sites were poorly quantified or even exhibited a net positive accumulation of O_2 thereby yielding unreliable respiration rates. As we could not differentiate between natural phenomenon and methodological error these values were excluded from our analyses. Reservoir means or values from neighbouring sites were substituted in such cases. Standard errors of the mean are provided with values given below.

Correspondence between estimated and measured CO_2 production in Eastmain-1

Estimates of total net CO_2 production for each station were made by summing benthic and water column (hypolimnetic and epilimnetic) respiration rates, and subtracting areal estimates of primary production. Calculated total net CO_2 production estimates for Eastmain-1 varied between 401 and 2875 mg C m^{-2} d^{-1} with an overall station mean of 1158 ± 138.7 mg C m^{-2} d^{-1} (Table 2), a value similar to the mean surface CO_2 emissions measured using floating chambers at the same stations over the same time periods (1422 ± 146 mg C m^{-2} d^{-1}). This agreement is particularly fitting considering that floating chambers tend to overestimate fluxes (Vachon et al., submitted). Furthermore, total net CO_2 production estimates among stations were strongly positively related to measured CO_2 surface fluxes at the same stations (Fig. 2), thereby providing compelling evidence that our quantitative estimates of the components of CO_2 production (benthic, hypolimnetic, and epilimnetic) are robust and realistic. Results on the spatial distribution of these components are reported below.

Figure 2. Estimated total net CO_2 production by measured surface CO_2 flux (station means; t-test, $r^2 = 0.64$, $p < 0.01$). Error bars represent the standard error of the mean for sites where more than one estimate of total net CO_2 production was available.



Hypolimnetic and benthic CO_2 production, the role of the flooded landscape

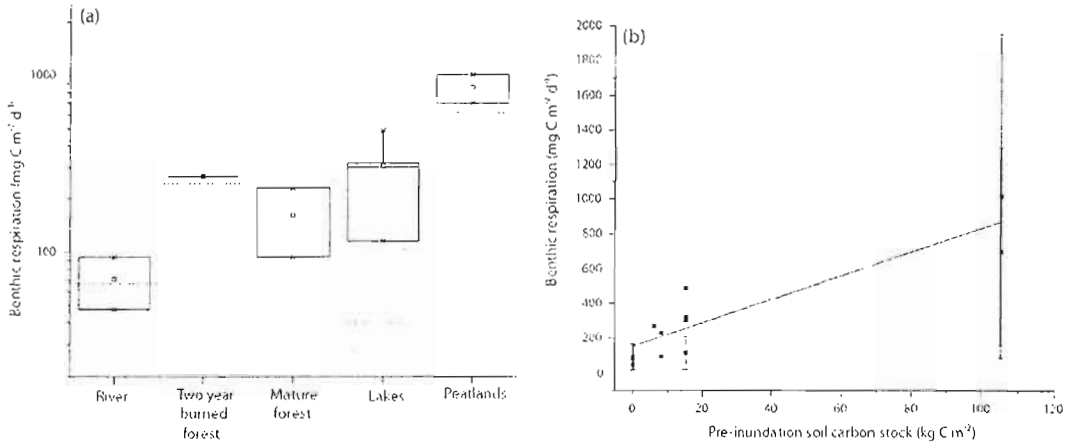
Accumulation rates of hypolimnetic CO_2 are the result of metabolism occurring at the benthic level as well as the water column, the latter potentially influenced by organic matter released by the benthic substrate. Hypolimnetic CO_2 accumulation rates, which differed significantly throughout the reservoir without expressing a direct, specific relationship with the pre-inundation carbon stock of a given landscape (Table 2), were roughly equivalent between the aquatic landscapes, with a mean value of 45.2 ± 9.1 mg C m^{-3} d^{-1} at flooded lakes and 39.2 ± 2.8 mg C m^{-3} d^{-1} in the Eastmain River channel. With a total mean value of 114.4 ± 37.8 mg C m^{-3} d^{-1}, forests had generally higher rates of hypolimnetic CO_2 accumulation than aquatic environments, yet varied significantly between specific forest types. This may be partly due to the fact that sample sizes were most restricted for forest sites, which tended to be the shallowest and least stratified sites, thus making consecutive profiles more difficult to analyse. The highest observed rates of hypolimnetic CO_2 accumulation were in the waters overlying carbon-rich peatlands, which had a mean value of 136.6 ± 3.4 mg C m^{-3} d^{-1}.

By subtracting hypolimnetic water column respiration from the accumulation of hypolimnetic CO_2, we obtained estimates of benthic respiration for individual flooded landscape types. Stations in which the accumulation of hypolimnetic CO_2 was too low to be explained by hypolimnetic water column respiration rates alone were excluded in order to minimize the inclusion of sites in which thermal stratification had been disturbed between sampling campaigns. Estimates of benthic respiration (provided in Table 2) were lowest at the flooded Eastmain River channel, at 70.9 ± 23.1 mg C m^{-2} d^{-1}. Although estimates of benthic respiration were unattainable for the 17 year burned forest landscape, two year burned forests (287 mg C m^{-2} d^{-1}) and mature forests (162.6 ± 68.1 mg C m^{-2} d^{-1}) had the next highest benthic respiration rates. Benthic respiration rates over flooded lakes (306.8 ± 76.3 mg C m^{-2} d^{-1}) were significantly higher than those in the Eastmain River channel, though the highest observed in the reservoir were over flooded peatlands (858.4 ± 158.4 mg C m^{-2} d^{-1}). We found a significant positive relationship between observed benthic respiration rates and pre-inundation sediment/soil respiration rates (Fig. 3a, Table 1) as well as with carbon stock (Fig. 3b, Table 1).

Landscape-derived heterogeneity in water column processes

The concentrations of DOC in profundal waters generally reflect trends in pre-inundation carbon stocks between landscapes (Table 2, Fig. 4a). While the rates of change in hypolimnetic DOC during periods of stable stratification varied widely, they displayed similar general differences between associated landscape types (Fig. 4b). Mean values were consistently negative (suggesting the possible dominance of DOC consumption over production within the hypolimnion), and were greatest over peatlands (-28.9 ± 6 mg C m^{-3} d^{-1}), followed by forest landscapes (-9.8 ± 0.7 mg C m^{-3} d^{-1} in two year burned forests, -13.2 ± 7.5 mg C m^{-3} d^{-1} in 17 year burned forests, and -11.5 ± 15.4 mg C m^{-3} d^{-1} in mature forests excluding two outliers). Sites overlying the flooded river channel (-3.7 ± 0.8 mg C m^{-3} d^{-1}) and flooded lakes (-2.4 ± 2.9 mg C m^{-3} d^{-1}) exhibited the lowest rates of DOC loss during stratified periods.

Figure 3. Estimated benthic respiration rates by (a) landscape type (t-test, $p = 0.03$, $\log_{10}$ transformations of station means) and (b) pre-inundation soil carbon stock. Horizontal dotted lines represent pre-inundation sediment/soil respiration rates (available in Table 1). The linear relationship between estimated benthic respiration and pre-inundation soil carbon stock is defined as BR (mg C m^{-2} d^{-1}) = 151.7 + (6.8 x Carbon Stock (kg C m^{-2})), $r^2 = 0.81$, $p = 0.0001$. Error bars represent the standard error of the mean for sites where more than one estimate of benthic respiration was available.



Water column respiration rates showed a considerable degree of variability between landscapes in the epilimnion as well as profundal waters, but did not increase with rising pre-inundation carbon stock values (Fig. 5, Table 2). In general, forest landscapes exhibited the highest water column respiration rates. Profundal water column respiration rates often fell within the same range of values measured for epilimnetic respiration rates despite generally lower temperatures.

Total surface CO_2 emissions slightly increased with the carbon stock of the underlying flooded landscape, though the difference between landscapes was not statistically significant (Table 2, $p = 0.95$).

Figure 4. Dissolved organic carbon (DOC) (a) concentrations and (b) rates of change in hypolimnetic waters, by landscape type. Two outliers are not included in 4(b), for mature forests, with rates of 1604 and -1686 mg C m^{-3} d^{-1} at the same site, both linked to a single outlying measurement of DOC. Landscape types are organized, ascending from left to right, in order of each landscape's estimated pre-inundation carbon stock.

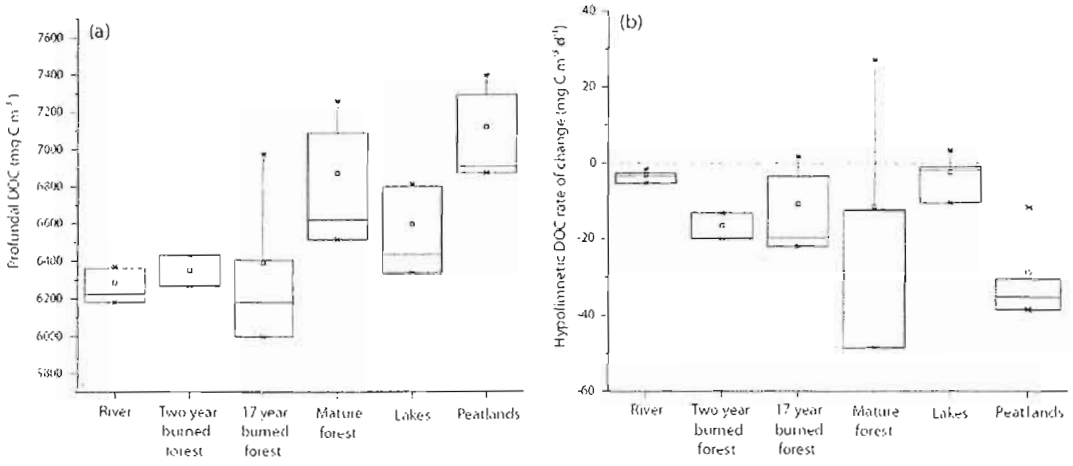


Figure 5. Epilimnetic (boxes) and mean profundal (columns) water column respiration rates by landscape type. Landscape types are organized, ascending from left to right, in order of each landscape's estimated pre-inundation carbon stock.

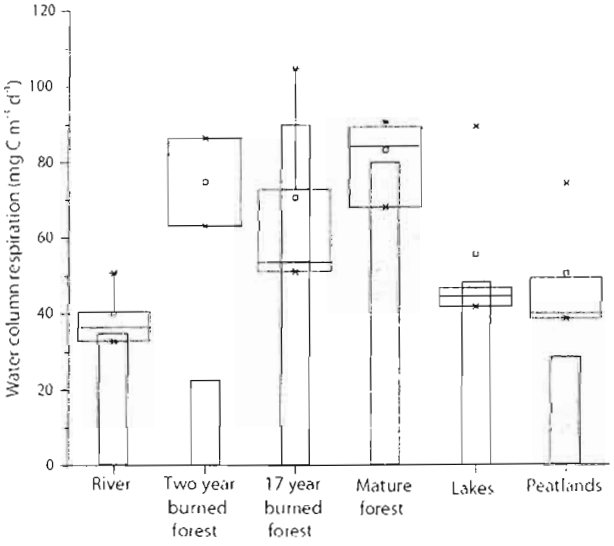


Table 2. Measured and estimated variables by flooded landscape type.

Flooded landscape type	Hypolimnetic CO_2 accumulation (mg C m^{-3} d^{-1})	Benthic respiration (mg C m^{-2} d^{-1})	Hypolimnetic water column respiration (mg C m^{-3} d^{-1})	Epilimnetic water column respiration (mg C m^{-3} d^{-1})	Total net CO_2 production (mg C m^{-2} d^{-1})	Surface CO_2 flux (mg C m^{-2} d^{-1})	Profundal dissolved organic carbon (mg C m^{-3})
Eastmain river channel	39.2 ± 2.8 (n = 4)	70.9 ± 23.1 (n = 2)	33.8 ± 0.4 (n = 2)	40.2 ± 3.9 (n = 4)	987.8 ± 131.6 (n = 2)	1254 ± 45.1 (n = 4)	6285 ± 47.4 (n = 4)
Two year burned forest	122.5 (n = 1)	268.4 (n = 1)	23.4 ± 22.1 (n = 2)	74.8 ± 11.6 (n = 2)	401 (n = 1)	1402 ± 233.4 (n = 2)	6351 ± 81.2 (n = 2)
17 year burned forest	28.2 ± 8.6 (n = 2)	-----	133 ± 16 (n = 2)	70.7 ± 12.4 (n = 4)	-----	1363 ± 312.8 (n = 4)	6393 ± 212.5 (n = 4)
Mature forest	196.5 ± 1.2 (n = 2)	162.6 ± 68.1 (n = 2)	104.4 ± 21.8 (n = 3)	83.2 ± 5.2 (n = 4)	1038 ± 90.5 (n = 2)	1366 ± 165.5 (n = 4)	6872 ± 179.5 (n = 4)
Mean of forest landscapes	114.4 ± 37.8 (n = 5)	214.8 ± 15.9 (n = 2)	115.8 ± 14.7 (n = 5)	76.5 ± 5.6 (n = 10)	641.4 ± 310 (n = 2)	1372 ± 133.9 (n = 10)	6576 ± 130.3 (n = 10)
Lakes	45.2 ± 9.1 (n = 4)	306.8 ± 76.3 (n = 4)	47.7 (n = 1)	55.7 ± 11.3 (n = 4)	1220 ± 232.8 (n = 4)	1234 ± 197.2 (n = 4)	6597 ± 123 (n = 4)
Peatlands	136.6 ± 3.4 (n = 2)	858.4 ± 158.4 (n = 2)	27.9 ± 3.6 (n = 3)	50.6 ± 8.2 (n = 4)	1705 ± 266.9 (n = 2)	1468 ± 101.8 (n = 4)	7119 ± 133.3 (n = 4)
Eastmain-1 mean	78.8 ± 16 (n = 15)	334.5 ± 89.7 (n = 11)	70.7 ± 14.6 (n = 11)	61.4 ± 4.6 (n = 22)	1158 ± 138.7 (n = 11)	1343 ± 71.7 (n = 22)	6626 ± 86 (n = 22)

Note. Flooded landscape types are organized, top to bottom, in order of increasing estimated carbon stock. Mean station values are used in calculating landscape means.

Discussion

Presence of a landscape-derived benthic heterogeneity

With the sole exception of flooded lakes, estimated benthic respiration rates in all landscapes were roughly equivalent to sediment or soil respiration rates prior to inundation. Elevated estimates of benthic respiration rates over lakes could be attributed to the possible proximity of peatlands to natural lakes in the boreal landscape (which could significantly influence the accumulation of CO_2 within a shared hypolimnetic environment), or they may reflect the possibility that lakes could be a primary site of the deposition of rich organic carbon when the reservoir is first inundated, being generally deep sites which would experience low currents (Teodoru et al., submitted).

While our estimates of benthic respiration include all CO_2 production occurring along the benthic environment, the decomposition of vegetation is not considered in given pre-inundation sediment and soil respiration estimates, leading to possible differences in estimates depending on the quantity and duration of decaying vegetation. Research on another boreal reservoir has indicated that the majority of highly labile foliage decays within the first few years of a reservoir's inundation, while less-labile wood or shrubs continue to decay over longer periods of time (Matthews et al., 2005). This indicates that flooded foliage was not likely a significant source of CO_2 during the period of our study, though wood or shrubs which remained anchored to the soils may have contributed to our estimates of benthic respiration for flooded terrestrial environments. Coupling vegetative decay rates with soil respiration rates, the proportional contribution of the benthic environment to CO_2 emissions may be greatest in the first years after a reservoir's inundation. This conclusion is in line with a prior study of Eastmain-1, which determined the proportional influence of benthic CO_2 production as decreasing in the first three years after inundation (Teodoru et al., submitted).

Benthic influence on the water column

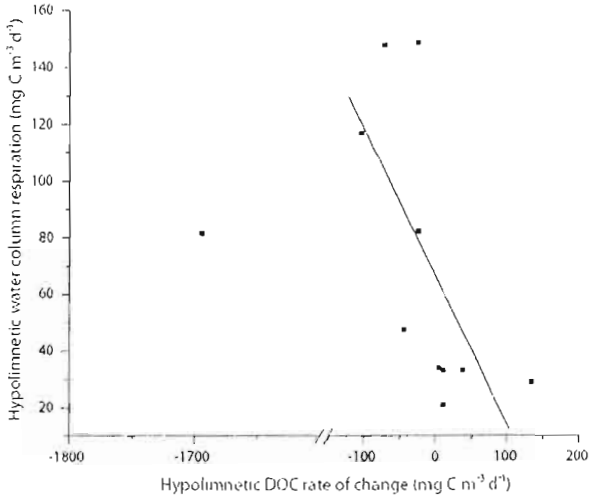
DOC concentrations and rates of decline were significantly and directly related to the carbon stock of flooded landscapes. This strongly suggests that the amount and nature of the hypolimnetic DOC in the reservoir is not only derived from the main Eastmain River inflow, but is also influenced by the flooded landscape, likely as the result of DOC released from the various benthic environments. Furthermore, a significant negative relationship was found to exist between the hypolimnetic DOC rate of change and the water column respiration rate in the hypolimnion (Fig. 6). Thus, stations with rapid DOC consumption also exhibited elevated water column respiration rates, as expected. We then applied this relationship in order to calculate estimates of hypolimnetic water column respiration throughout the reservoir. This approach provided us with a means to obtain first-order estimates of the rate of DOC release from flooded terrestrial landscapes and how it varied among landscape types. Assuming that the lability of imported Eastmain River organic carbon can be considered uniform within the reservoir (based on the fluvial character of the aquatic system, and the moderate estimated residence time of 145 days provided by Teodoru et al., submitted), we calculated the benthic DOC release rate as:

(5) $DOC_{release} = (\Delta DOC_{hypo} + (WCR_{hypo} - DOC_{lab}))*Z_{hypo}$

where $DOC_{release}$ is the rate at which DOC is released from a flooded environment into the water column (in mg C m^{-2} d^{-1}), ΔDOC_{hypo} is the measured rate of change for DOC in the reservoir hypolimnion over periods of stable stratification (in mg C m^{-3} d^{-1}), WCR_{hypo} is the water column respiration rate in the hypolimnion (in mg C m^{-3} d^{-1}), DOC_{lab} is the estimated base rate of DOC lability in the Eastmain River (in mg C m^{-3} d^{-1}), and Z_{hypo} is the hypolimnetic thickness at a given site (in m). Given the lack of available information on lability or rates of DOC consumption in large river systems, a value of 15 mg C m^{-3} d^{-1}, derived from a study of the Hudson River, USA, is here applied for DOC_{lab} (del Giorgio and Pace, 2008). According to these calculations, the overall benthic DOC release rate from terrestrial environments averaged 183.4 ± 28.7

mg C m^{-2} d^{-1} during periods of stable stratification. Estimated for flooded terrestrial environments separately, peatlands (mean value 241 ± 62.4 mg C m^{-2} d^{-1}) and mature forests (mean value 228.1 ± 76.8 mg C m^{-2} d^{-1}) were found to exhibit the highest rates of DOC release into the hypolimnion. Two year burned forests (94.2 ± 22.1 mg C m^{-2} d^{-1}) and 17 year burned forests (132 ± 27.6 mg C m^{-2} d^{-1}) exhibited the lowest rates of DOC release. These estimates are important as they show that the flooded benthic environment has two separate roles on the metabolism of a newly created reservoir. It is a site of elevated organic carbon mineralization directly liberating CO_2 to the hypolimnion, yet it also releases substantial quantities of DOC, a portion of which will itself be decomposed in the water column. As averages for the Eastmain-1 Reservoir, we found that 359.6 ± 96.7 mg C m^{-2} d^{-1} is released from the benthic environment as CO_2, but a further 183.4 ± 28.7 mg C m^{-2} d^{-1} (roughly 50%) is released from terrestrial environments as DOC. The extent to which this DOC is ultimately labile will require further study.

Figure 6. Hypolimnetic water column respiration in relation to hypolimnetic ΔDOC. The single outlier, taken from a relatively shallow (8m) mature forest site, was not included in the calculation of a linear relationship between variables. The linear relationship, used in describing estimates of DOC release from different landscapes, is described by the equation $WCR_{hypo} = 65.8 - (0.517 \times \Delta DOC_{hypo})$ ($r^2 = 0.44$, $p = 0.04$).



Applicability to reservoir surface CO_2 emissions

By combining estimates of benthic respiration, water column respiration, and primary production, we have shown it is possible to reconstruct surface CO_2 emissions at a particular reservoir site that match remarkably well those actually measured using floating chambers. However, it is notable that the landscape-derived signal becomes increasingly difficult to discern at the level of surface CO_2 emissions, which may be due to horizontal diffusion of CO_2 in the water column, as well as the relationship between surface fluxes and other factors such as mixing events and thermal stratification. Horizontal advection of water is generally more prevalent than the vertical transport of water at a given reservoir site (Duchemin et al., 1995). This suggests that the relationship we observed between surface CO_2 emissions and our reconstructed total net CO_2 production does not imply a direct vertical transport of CO_2 through the water column, but rather that landscape-derived traits in the benthic and water column environments, measured along a given vertical profile, may be considered uniform at the scale of the landscape, and furthermore that observed surface CO_2 emissions may be considered reflective of the CO_2 produced and consumed at the scale of the landscape.

Conclusions

This study supports the notion that large differences in carbon stock between different landscapes can significantly influence the quantity of CO_2 produced and emitted from a young reservoir. Where previous research has indicated that the water column of Eastmain-1 is an important source of the system's total CO_2 emissions (Lalonde, 2009; Brothers et al., submitted; Teodoru et al., submitted), this study indicates the degree to which individual flooded landscapes influence pCO_2 and respiration rates in the overlying water column. Furthermore, this study begins to reveal the significance of DOC release from flooded environments, which may explain previously observed elevated respiration rates in the hypolimnion and epilimnion of the water column. Given previous studies which have implied that

flooding peatlands may result in long-term elevated CO_2 emissions (possibly lasting over 2000 years; Kelly et al., 1997), and a study which found similar benthic CO_2 emissions in 17 and two year old boreal reservoirs (Duchemin et al., 1995), it is possible that the trends observed in the present study may represent typical long-term conditions for boreal reservoirs.

Coupled with previous research indicating that the proportional contribution of the benthic environment and the water column towards surface CO_2 emissions in a young reservoir may reflect natural landscape characteristics (Brothers et al., submitted), this research may be applied to obtain first-order estimates of reservoir CO_2 emissions prior to inundation. As estimates rely upon readily accessible and common variables (soil carbon stock and sediment/soil respiration rates) these findings may lend themselves as well to reservoirs beyond the boreal zone.

Conclusion

The goal of this research is to further our understanding of reservoirs with the hopes that this knowledge will contribute to more informed planning of future hydroelectric schemes. This goal was met in two stages; the first stage places the metabolic components of a young boreal reservoir into the regional context of natural lakes, and the second stage details the influence of a flooded landscape on the benthic environment, water column, and surface CO_2 emissions of the same reservoir. This thesis may be considered a regional analysis of carbon cycling in a boreal reservoir, yet the broad nature of the factors identified as influencing surface CO_2 emissions (soil carbon stock and pre-inundation soil respiration rates) make these findings potentially applicable to a large range of reservoirs.

The findings of the first chapter of this thesis indicate that respiration in the water column and benthic environments are both significantly higher in a young boreal reservoir (Eastmain-1) than in natural lakes. Furthermore, the proportional contribution of the water column and benthic environment towards a system's total CO_2 production is found to be roughly equivalent in artificial and natural system types. While the surface area of Eastmain-1 is two orders of magnitude larger than the mean surface area of sampled nearby lakes, the site depths in Eastmain-1 and sampled lakes were more similar (limited in both system types to sites generally greater than 7m deep, the usual observed thermocline depth). This suggests that, while an inundated landscape may influence the total intensity of CO_2 production by supplying the water column with dissolved organic carbon (DOC) and nutrients, the reservoir's morphology may be more likely to determine the metabolic balancing between the CO_2 contribution of the water column or benthic environment. As this study primarily relies upon data from one year of measurements, two years after the reservoir has been flooded, this conclusion may be considered tentative and open to more detailed future analyses.

The second chapter of this thesis builds primarily upon the first chapter (which found the water column of Eastmain-1 to be an important source of CO_2

production) and a previous study (Teodoru et al., submitted) which identified a landscape signature in water column respiration rates and surface CO_2 emissions in the first years after the inundation of Eastmain-1. This chapter focuses primarily on processes occurring at the benthic layer, and finds benthic respiration rates at different flooded sites to be frequently similar to pre-inundation sediment or soil respiration rates at those same sites. Furthermore, the influence of individual flooded landscapes on the overlying water column is explored in terms of an observed spatial heterogeneity in rates of DOC consumption within the hypolimnion, and release from flooded terrestrial environments. It is determined that the character of a landscape influences not only benthic respiration rates, but the interactions between the benthic environment and water column (with regards to DOC release) and, ultimately, surface CO_2 emissions. Finally, this second chapter demonstrates that such independently-derived estimates of benthic respiration, water column respiration, and primary production can be used to accurately predict measured surface CO_2 emissions.

Together, the chapters of this thesis indicate that the water column of the Eastmain-1 Reservoir is a major source of the system's CO_2 emissions into the atmosphere. As Eastmain-1 may be considered a typical hydroelectric reservoir in the boreal zone of Canada (in terms of its size and the variety of landscapes it has inundated), this conclusion calls for a departure from the standard assumption that benthic environments monopolize CO_2 production in hydroelectric reservoirs. Furthermore, this research provides simple tools by which rough estimates of carbon emissions from planned reservoirs may be made, based on the carbon stock, areas of flooded landscapes, and the predicted depth of a reservoir. Research remains to be done in this field, especially in testing the applicability of these findings to other reservoirs in the boreal zone and other regions. Still, this thesis advances our knowledge on several fundamental issues concerning carbon cycling in reservoirs, and may provide a useful starting point for future research on the subject.

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